Dynamics of forest ecosystem properties and resilience in a temperate woodland undergoing dieback

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For Catherine, my best friend and wife,

with whom I shared this journey and many others.

Thesis abstract

Given that woodland disturbance events are expected to become more frequent and severe in the future, it is crucial to understand how fundamental underlying ecosystem properties (EPs) including biodiversity, ecosystem functions and ecosystem services will be impacted. Currently, this knowledge is severely limited, but is essential for future management of forests at both stand and landscape scales. The impact of such disturbances on EPs can be quantified through the use of ecological resilience and its associated concepts. Resilience relates to either the amount of disturbance an ecosystem can endure and still exist or the degree to which an ecosystem can resist or recover from disturbance. Resilience concepts of ecological thresholds, points of abrupt change in an EP, and resistance, persistence and recovery time are useful metrics to determine disturbance impacts. Moreover, using knowledge of how EPs are affected by disturbance, resilience assessments can enable inference of the current level of resilience that woodland has. The objectives of this thesis were therefore: 1) to determine how biodiversity, ecosystem functions and condition were affected in a forest undergoing dieback; 2) to examine the effectiveness of rapid condition assessment tools as a proxy use for inferring woodland resilience; and 3) to determine whether woodland cover influences resilience of EPs at a landscape scale.

The changing condition and extent of the New Forest provided an opportunity to measure EPs across a gradient of changing condition. This was carried out through gradient analysis of dieback, based on basal area decline, at the stand scale. Using the results obtained from the gradient analysis: i) the resilience of important woodland EPs was assessed at the landscape scale using simulations of different intensities of disturbance and woodland cover, which was used as a proxy for connectivity; and ii) commonly-used forest condition assessment tools, specifically airborne lidar and the woodland Common Standards Monitoring condition assessments, were tested to determine how effective they were and whether they could be used to infer resilience at the stand scale. Overall, evidence provided in this thesis suggests that: biodiversity and functional thresholds exist as the forest degrades; current condition assessment tools are not very effective at detecting variation in woodland condition and therefore are not sufficient to infer current resilience; and woodland cover influences the resilience of important woodland EPs, at the landscape scale. All the findings are discussed in context of the New Forest, an ecologically and socio-economically important landscape.

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CD5.8	Details for the GLM models for resistance in Chapter 5 with 0% WC excluded.
CD5.9	Details for the GLM models for persistence in Chapter 5 with 0% WC excluded.
CD5.10	Details for the GLM models for recovery time in Chapter 5 with 0% WC excluded.
CD5.11	Graphs of ecosystem property dynamics for Chapter 5.
CD5.12	Animated clips of LANDIS-simulated forest succession for the scenarios in Chapter 5.

Additional material on CD

AM_CD1	A version of the manuscript, supplementary material and figures resubmitted to *Scientific Reports*, which is in review. This is an edited version of Chapter 2.
AM_CD2	A version of the manuscript "*Quantifying future resilience of a temperate forest undergoing dieback*", which is in review. I am one of the co-authors of this manuscript; I helped to collect some of the field-collected data as part of my PhD.
AM_CD3	The manuscript "*Stand dieback and collapse in a temperate forest and its impact on forest structure and biodiversity*" that has been published in *Forest Ecology and Management.* I am one of the co-authors of this manuscript; I helped to collect some of the field-collected data as part of my PhD.
AM_CD4	A version of the manuscript "*Analysis of ecological thresholds in a temperate forest undergoing dieback*", which is in review. I am one of the co-authors of this manuscript; I helped to collect some of the field-collected data as part of my PhD.
AM_CD5	The Forest Research report, "*Exploring the use of metabarcoding as a biomonitoring tool to detect critical thresholds of habitat cover for woodland-dependent arthropods along a gradient of beech forest dieback*", of which I am a co-author; I set-up the plots and helped to collect the field-collected data as part of my PhD.

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Last, but definitely not least, I thank Catherine Titley (Evans) who always made time to listen to my witterings and proofread my thesis, as well as giving me confidence in my work and myself.

Author's declaration

I confirm that all aspects of this thesis are my own work with the exceptions stated below.

Chapter 2: this Chapter has been resubmitted following suggestions from manuscript reviewers. Therefore, it should be published in *Scientific Reports* soon as: Evans, P. M., Newton, A. C., Cantarello, E., Martin, P., Sanderson, N., Jones, D., Barsoum, N., Cottrell, J. E., A'Hara, S. W. and Fuller, L., 2017. Thresholds of biodiversity and ecosystem function in a forest ecosystem undergoing dieback.

As lead author on the above manuscript, I led most aspects including study development, data collection, data analysis and manuscript preparation. However, the ground-dwelling arthropod data was collected by Forest Research, the ectomycorrhizal fungi data by Adrian Newton and the lichen data by Neil Sanderson, who all kindly let me use their respective data. A version of the submitted manuscript that has had additional input from the co-authors is available in the Additional Material on the attached CD (AM_CD1).

Chapter 4: the lidar data used in this Chapter was processed by Ross Hill, who kindly allowed me to use the data in my thesis.

Definitions/ Glossary

Disturbance	Events that disrupt the structure of an ecosystem and/ or its communities and therefore have a major influence on ecosystem dynamics.
Ecosystem services	The benefits people derive from natural systems.
Ecological resilience	An ecosystem's capacity to absorb disturbance and change and still persist, which is based on the assumptions of multiple stable states.
Ecological threshold	The point at which a small change in environmental conditions leads to a non-linear change in an ecosystem's state variable.
Ecosystem properties	Properties of an ecosystem, which includes biodiversity, ecosystem services and ecosystem functions.
Engineering resilience	The degree to which an ecosystem property can resist or recover from disturbance.
Multiple stable states	When an ecosystem can exist in more than one stable state, exhibiting long-term stability under the same set of environmental conditions.
Persistence	The extent to which an ecosystem or community continues over time after being disturbed.
Recovery time	The time after which the ecological state or property has returned to its pre-disturbance value.
Resistance	Change in an ecological state or property caused by a disturbance.
Stable state	When community dynamics and ecological processes remain in equilibrium over an extended timescale.
Succession	The directional and continual change of biological communities over time.

Acronyms

A&O	Ancient and Ornamental woodlands.
AR	All returns.
BA	Basal area.
CA	Condition assessment.
CSM	Common Standards Monitoring.
EP	Ecosystem properties.
ES	Ecosystem services.
FR	First return.
GLM	Generalised linear models.
IPCC	Intergovernmental Panel on Climate Change.
IUCN	International Union for Conservation of Nature.
JNCC	Joint Nature Conservation Committee.
MEA	Millennium Ecosystem Assessment.
MSS	Multiple stable states.
NEA	National Ecosystem Assessment.
NEWP	Natural Environment White Paper.
NP	National Park.
PA	Protected Areas.
PDI	Pulse disturbance intensity.
SAC	Special Area of Conservation.
SSSI	Site of Special Scientific Interest.

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Chapter 1:
Introduction

1.1. Global forest loss and degradation

Rapid environmental changes and human activity are widely recognised as having an irreversible effect on wildlife and the environment at a global scale (Foley et al. 2005; MEA, 2005; Pimm et al. 2014). In wooded ecosystems specifically, the greatest direct effect that human activity has is through deforestation (Lanly, 2003; Rudel et al. 2005; van der Werf et al. 2009; Hansen et al. 2010, 2013; Laurance et al. 2014), which refers to large-scale tree clearance where less than 30% of the original canopy cover remains (Lanly, 2003). Deforestation of any wooded habitat causes devastation to ecosystems by impacting physical, biological and chemical processes and properties, sometimes even causing total cessation of ecosystem functioning (DeFries et al. 2010). This has major consequences locally and globally, which include modifications to climate, and an increased chance of extreme weather events and biodiversity extinctions (MEA, 2005; van der Werf et al. 2009; Fahrig, 2013; Melo et al. 2013).

In addition, ecosystem degradation, which is defined as an overarching impoverishment of an ecosystem, modifying the habitat as to reduce its condition, structure and functionality, but not necessarily the total area (Lanly, 2003), is also having an unprecedented global impact on forest properties (Peres et al. 2006; Ahmed, 2008; Spilsbury, 2009; Hansen et al. 2013; Haddad et al. 2015; Allan et al. 2017). Woodland degradation is often caused by environmental changes and anthropogenic activities, the effects of which include the loss of ancient forest functions, simplification of forest structure and decreases in size of high quality forest patches combined with increasing patchiness and therefore isolation of remnant woodland (Noss, 1999). In the tropics, 2.3 million hectares of forest were ‘visibly’ degraded per annum in the years before 1997, in addition to 5.8 million hectares deforested (Achard et al. 2002). In some locations, areas of degraded forest span more than double that of deforested areas (INPE (2005), cited in Peres et al. 2006).

1.1.1. Implications for biodiversity

A sixth mass extinction of biodiversity, the number and abundance of species that exist in a given area, is proposed to be occurring globally (Butchart et al. 2010; Pimm et al. 2014). The extinction rate is predicted to be declining at a thousand times the normal rate, based on the fossil record (MEA, 2005). Together with other drivers including land-use

change and over-exploitation (Worm et al. 2006), deforestation and woodland degradation are two of the major causes leading to high levels of global extinction (MEA, 2005; Butchart et al. 2010; Dirzo et al. 2014; Pimm et al. 2014). In the case of Singapore alone, which has lost 95% of its wooded cover, at least 28%, possibly reaching as much as 50%, of the overall biodiversity has been extirpated (Brook et al. 2003). Additionally, 60% of species in the Brazilian Amazon are predicted to become extinct within the next 40 years if the deforestation continues at the current rate (Wearn et al. 2012). As biodiversity is integral to the multi-functionality of an ecosystem, being essential for the dynamic regulation of that ecosystem (Naeem et al. 1999; Balmford et al. 2008; Cardinale et al. 2012; Mace et al. 2012), knock-on effects of biodiversity loss include major modifications to ecosystems processes and human well-being (Diaz et al. 2006; Cardinale et al. 2012).

1.1.2. Implications for ecosystem services and functions

Biodiversity, ecosystem processes and well-being are connected through the benefits people derive from natural systems, which are known as ecosystem services (ES), as illustrated in Fig. 1.1. ES are the benefits derived from both the functioning of ecosystems and the end-products provided (Costanza et al. 1998; Muradian, 2001; de Groot et al. 2002; Hooper et al. 2005; MEA, 2005; Balmford et al. 2008). ES are split into four categories: regulatory, provisioning, cultural and supporting services (MEA, 2005). For a full description of ES and differences uses of ES terminology, see de Groot et al. (2002) and Hooper et al. (2005).

Forests and woodlands are of particular importance for ES provisions as they provide the greatest multi-functionality of any habitat (Haines-Young and Potschin, 2008), making them of exceptional significance to human well-being. Thus, deforestation and degradation significantly impact ecosystem processes and ES provisions (Chazdon, 2008). This results in the loss and degradation of essential ES and ecosystem functions including nutrient cycling, carbon sequestration, water cycling and soil formation, all of which are crucial functions underlying all other processes (Foley et al. 2007; Binkley and Fisher, 2012). Also affected are ES provisions of which wooded ecosystems are largely responsible, which include the avoidance of climate stress and hazards, pest control, noise reduction, and habitat provision for a highly diverse genetic pool (Pearce and Moran, 1994; Nowak and Dwyer, 2007; Bonan, 2008; Patterson and Coelho, 2009; NEA, 2011).

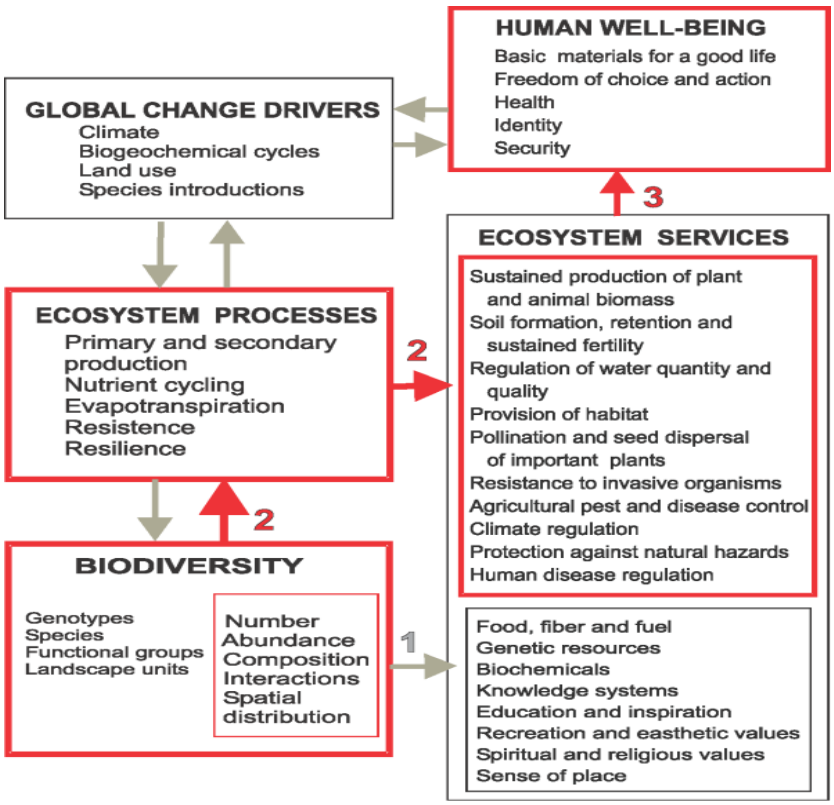

Fig. 1.1: Schematic representing the links between ecosystem functions, ecosystem services, biodiversity and human well-being. The arrows represent influence from one category to another. The functioning of an ecosystem fits within the 'ecosystem processes' box. Reproduced from Díaz et al. (2006).

1.1. Forests as dynamic systems

The flora, fauna and microbes present within an ecosystem are essential for the dynamic regulation of that ecosystem; the interactions between soil, water and vegetation perform critical processes to maintain productivity and biological and chemical conditions of that ecosystem (Naeem et al. 1999; Folke et al. 2004; Hooper et al. 2005; Duffy, 2009; Cardinale et al. 2012; Hooper et al. 2012; Gamfeldt et al. 2013).

One prominent example of a dynamic process in forests, as with other ecosystems, is nutrient cycling. Nutrient cycling involves the regulation and conversion of essential nutrients, including nitrogen, carbon, phosphorus and sulphur, from mineral or atmospheric forms to those that can be utilised by organisms for repair, growth and maintenance (Attiwill and Adams, 1993; Luo et al. 2004). The nutrient cycling process is dynamic as quantities of certain nutrients enable forests to function, while quantities of other nutrients limit the rate of other cycles (Ashman and Puri, 2002; Vitousek et al. 2002; Galloway et al. 2004; Luo et al. 2004). For example, nitrogen is obtained by plants from the soil and is used mostly for photosynthesis, which has a major impact on productivity and primary production (Vitousek et al. 2002; Galloway et al. 2004; Ashman and Puri,

2008). Greater productivity then increases carbon cycling, storage and sequestration and water cycling, creating a feedback at local and global levels (Stuart and Edwards, 2006; Bonan, 2008; Malhi et al. 2008). However, the amount of carbon present in the soil can also limit the rate of processes that involve nitrogen such as plant growth (Luo et al. 2004).

1.1.1. Role of succession

Succession, the directional and continual change of biological communities over time (Finegan, 1984), is one of the main determinant factors underpinning the dynamic processes of forests, as it governs local composition, structure and functional diversity (DeWalt et al. 2003). While the precise mechanisms guiding succession are debated (see competing theories in Connell and Slatyer (1977); Finegan, (1984)), successional pathways are integral to understanding how large-scale changes occur in variables such as species richness and composition, as well as the structure and dynamics of ecosystems (Prach and Walker, 2011).

The general direction of succession is from initial colonising plants to old-growth forest (Angelstam, 1998). Succession is categorised into two types: primary and secondary. Primary succession occurs when biological communities begin to establish and grow in a location where no biological life existed previously. For example, where lava flow or sand dune accumulation may have occurred. Secondary succession occurs after a biological community has been disturbed, allowing new plants to colonise that area. The recolonisation of trees and other plants after storms or fire is therefore considered secondary succession; early successional plants can establish due to the new conditions created, initiating a new successional pathway (Finegan, 1984; Packham et al. 2001).

1.1.2. Role of disturbance

Modifications to successional pathways arise from ecological disturbances, which are events that disrupt the structure of an ecosystem and/ or its communities and therefore have a major influence on ecosystem dynamics (Pickett and White, 1985). Disturbances are often essential to the longevity of ecosystems, as they maintain diverse structures through the alleviation of competition and creation of heterogeneity (Pickett and White, 1985; Dale et al. 2001).

Disturbance events can be described as pulse or press, depending on the relative temporal duration of an event, and can be caused by biotic, including humans, or abiotic

factors. A pulse disturbance is a single event that causes a sudden change and lasts for relatively short time (Lenton, 2011; Barnosky et al. 2012; Scheffer et al. 2012). Windstorms, fires, resource extraction and deforestation (i.e. clear-cutting) are examples of pulse disturbances (Dale et al. 2001). A press disturbance is an event that has a continual impact over a relatively long temporal period (Dale et al. 2001; Packham et al. 2001; Begon et al. 2009). Thus, active herbivores that frequently disturb ecosystems through such activities as soil disturbance, trampling and grazing would be considered a press disturbance. Furthermore, the impacts of disturbance depend on its magnitude, duration, frequency and change over spatial and temporal scales (Donohue et al. 2013).

Underlying drivers and stressors can govern the disturbances which occur, these include the abiotic influence of climate change, prevailing weather conditions, hydrology, pollution, nutrient cycles, erosion and temperature (Dale et al. 2001). Biotic drivers meanwhile relate to dynamics of animal populations, pests and pathogens (Jones, 1945; Packham et al. 2001; Begon et al. 2009). Furthermore, the strength, frequency and temporal and spatial dynamics of disturbances define their influence within or upon an ecosystem (Pickett and White, 1985; Grimm and Wissel, 1997).

1.1.3. Role of gap-phase regeneration

When a tree dies or falls down, as a result of a disturbance or mortality event, a canopy gap may be created. As a result, previously suppressed saplings can start to grow in the space due to the increases in abiotic and biotic factors, such as light, temperature, nutrient availability, litter depth and microhabitats at different levels of the stand afforded by the lack of canopy (Dale et al. 2001; Kinzig et al. 2006; Bottero et al. 2011). This is known as gap-phase regeneration. Furthermore, different species can also colonise the space due to canopy gaps influencing the local functions and dynamics by increasing heterogeneity of the conditions within the stand (Uhl et al. 1988; Rentch et al. 2010). Thus, gap-phase regerenation and colonisation can alter the composition, structure, function and spatial structure of the forest (Grimm and Wissel, 1997; Dale et al. 2001; Kinzig et al. 2006; Bottero et al. 2011).

1.1.4. Role of modified disturbance regimes

In recent decades, natural, regulatory disturbance regimes have been severely altered by climate change and anthropogenic activity (e.g. deforestation, degradation, pollution), and the interactions between them (Milad et al. 2011). For instance, climate change and other anthropogenic disturbances have modified naturally occurring fire disturbance

patterns and temporal dynamics in some forests, resulting in much larger scale fire extents and longer durations (Dale et al. 2001; MEA, 2005; Alencar et al. 2015). Similarly, outbreaks of stand-destroying beetles have increased dramatically owing to climate change in boreal forests (Kurz et al. 2008; Raffa et al. 2008; Bentz et al. 2010), and climate-mediated pathogens are becoming more widespread in many forests, which has resulted in large scale tree mortality (Packham et al. 2001; Begon et al. 2009; Harvell et al. 2002; Santini et al. 2013).

Impacts of the modified disturbance regimes have been substantial, majorly affecting the biodiversity, structure and functioning of ecosystems (Pickett and White, 1985; Turner, 2010; Vanderwel et al. 2013), sometimes in completely novel ways (Mesquita et al. 2001; Prach and Walker, 2011). Moreover, they have the potential to create acute changes in ES and functions over short and long timescales (i.e. from years to centuries) (Turner, 2010), the consequences of which include the release of previously-sequestered greenhouse gases (e.g. carbon dioxide), biodiversity loss (Royo at el. 2010; Lavorel et al. 2014), and decreases in the size of terrestrial carbon sinks (Bonan, 2008; Pan et al. 2011).

1.1.5. Implications for forests

Given the increasingly severe nature of global threats, modified disturbance regimes, and changing dynamics impacting forests, rapid, large scale dieback of forests is being observed globally (Breshears et al. 2005; Huntingford et al. 2008; Kurz et al. 2008; Raffa et al. 2008; van Mantgem et al. 2009; Briske et al. 2010; Allen et al. 2015). Consequently, major transformations of forest ecosystems are predicted to be occurring (Mallik, 1995; Laurance, 1999; Thom and Seidl, 2016), including in temperate forests (van Mantgem and Stephenson, 2007; Lindner et al. 2010). For example, abrupt shifts in condition have been predicted for tropical forest regions as a result of interactions between climate change, precipitation amount, fire and browsing intensity (Hirota et al. 2011; Staver et al. 2011). As forests are such complex ecosystems, unpredictable and rapid changes would be disastrous, especially relating to ES provision (Casini et al. 2009) and biodiversity (Heller and Zavaleta, 2009; Hirota et al. 2011; Staver et al. 2011; Lavorel et al. 2014).

The UK National Ecosystem Assessment (NEA, 2011) indicates that the effects of climate change, combined with other altered disturbances regimes, will have a dramatic effect upon British woodlands. The most significant factor is theorised to be the increase in biotic threats such as has been seen in North America (Hicke et al. 2012). The NEA (2011) predicts: 1) large-scale modification of native woodland floral and faunal

assemblages will occur; 2) significant detrimental effects of recent summer droughts and wet winters will become apparent, with wind-throw and dieback having already increased; 3) intensifications in nitrogen deposition, which will lower fungal and lower plant diversity (Galloway et al. 2004); 4) UK forest growth is predicted to be reduced, along with carbon sequestration, owing to rising ozone concentrations; and 5) vulnerability to winter stresses will also rise.

1.2. Resilience

In response to the above concerns, both for the UK and globally, there has been a renewed focus on maintaining and promoting resilience of ecological systems and socio-ecological systems to reduce the vulnerability of those systems to changes (Scheffer et al. 2001; Biggs et al. 2012; Dai et al. 2012). This explains partially why 1% of all scientific ecological papers now include resilience (Hodgson et al. 2015). Consequently, national and international policies and management initiatives have adopted the use of the term resilience. Some prominent examples of this can be found in British (Lawton et al. 2010; Natural England, 2016), American (EPA, 2012), Australian (COAG, 2011) and African (The African Development Bank, 2013) strategies where the main aim is to improve the sustainability and health of countries. The enhancement of resilience is also featured as a goal in major international strategies, including the fifth assessment of Intergovernmental Panel on Climate Change (IPCC, 2014) and the Convention on Biological Diversity (Thompson, 2009). Despite the abundance of use of the term resilience in policy, it is seldom defined and thus its current use in policy and management lacks usefulness (Myers-Smith et al. 2012; Newton, 2016).

Many different and sometimes contradictory definitions of ecological resilience have come to exist in a scientific context. This has made the use of resilience in a purely ecological context difficult to interpret (Grimm and Wissel, 1997; Beisner et al. 2003; Brand and Jax, 2007; Newton, 2016). For instance, in a review of 234 publications referring to resilience, 66% of studies did not specify the explicit definition used (Myers-Smith et al. 2012). This confusion and ambiguity has undermined scientific and management quality since such management approaches including the adaptive governance framework – the recommended approach to resource management – is based on the notion of resilience (Holling, 1978; Gunderson and Light, 2006).

For the purpose of being able to use resilience in an operational way, and for clarity, this thesis will focus on two widely-used, complementary definitions of resilience: ecological resilience and engineering resilience, both of which are important to consider

as they provide different ways of assessing the resilience of natural systems. These are described in the following section, and the main differences between the two definitions are summarised in Table 1.1.

1.3.1. Definitions of resilience

1.3.1.1. Ecological resilience

As an ecological concept, resilience (herein referred to as ecological resilience) was originally defined by Holling (1973) as an ecosystem's ability to be able to maintain its structure and function while being perturbed. It is a measure of an ecosystem's capacity to absorb disturbance and change and still persist (Standish et al. 2014). This definition is often considered akin to adaptive capacity, i.e. the ability of an ecosystem to reconfigure while undergoing disturbance resulting in no significant changes in ecosystem properties (Carpenter et al. 2001).

The ecological resilience definition assumes that the prominent ecological theory of multiple stable states (MSS) is accurate. MSS hypothesises that ecosystems can exist in more than one stable state, exhibiting long-term stability under the same set of environmental conditions (Beisner et al. 2003). These states are considered stable in relation to community dynamics and ecological processes being in equilibrium over an extended timescale (Holling, 1973; Groffman et al. 2006).

Cup and ball models can be utilised as a visual way of representing the MSS concept (Beisner et al. 2003; Scheffer and Carpenter, 2003). In the heuristic (Fig. 1.2), the multiple stable states are the valleys, or 'domains of attraction', while the ball represents the current ecosystem state. If a disturbance occurs or environmental parameters alter, the ball that normally stays in the basin will be forced to another state; in absence of those changes, the ball naturally stays at the lowest point (i.e. the domain of attraction). In theory, the ball's movement can therefore be anticipated assuming all the stressors are known (Beisner et al. 2003), with the displacement indicating the strength and frequency of disturbance (Grimm and Wissel, 1997).

In MSS theory, an ecosystem should begin to transition between states if the ball exceeds a peak. This peak is also known as a threshold. Thus, ecological thresholds are points where transitions between states of an ecosystem result from small changes in conditions or drivers (Scheffer et al. 2001), denoted by the trajectory of an ecosystem state becoming modified, which may be difficult or impossible to reverse (Scheffer et al. 2001; Groffman et al. 2006; van Nes and Scheffer, 2007; Suding and Hobbs, 2009). If thresholds are exceeded, non-linear responses are posited to occur (Fig. 1.3b) (Scheffer

and Carpenter, 2003). Consequently, detections of sharp changes in an ecosystem state should be able to be identified (Petraitis and Hoffman, 2010; Scheffer et al. 2012). Therefore, the greater distance the ecosystem state property is from the threshold, the greater resilience that ecosystem property has (Scheffer et al. 2001; Folke et al. 2004; Briske et al. 2006; Scheffer, 2009; McClanahan et al. 2011; Standish et al. 2014; Newton and Cantarello, 2015). The opposing view to the theory of thresholds is the theory that ecosystem state declines linearly with the strength of a disturbance (Fig. 1.3a) (Suding and Hobbs, 2009; Scheffer et al. 2012).

A fundamental ingredient of ecological thresholds is a switch from a dominance of negative feedbacks to a dominance of positive feedbacks (Scheffer et al. 2012). Negative feedbacks within an ecosystem act to maintain its dynamic functionality, acting to reinforce local resilience (Rial et al. 2004; Briske et al. 2006). For example, due to the regular forest fires in some biomes the turnover of biodiversity is constant (Turner, 2010). Positive feedbacks promote propagation of multiple change creating a domino-like effect, where the system dynamics become increasingly disparate (Muradian, 2001; Fagre et al. 2009), i.e. self-exacerbating feedback. For instance, if fire occurrence increases too much, large-scale woodland fire regimes could feedback positively, altering precipitation patterns which allow for more fires (Adams, 2013). In forest systems, degradation to ecosystem structure and composition, soil erosion rates, water and nutrient cycles and local climate have been included in predictions of abiotic feedback mechanisms creating thresholds (Briske et al. 2006; Raffa et al. 2008).

If thresholds exist, exceeding one may provide significant future management challenges (Eiswerth and Haney, 2001; Fagre et al. 2009). This is due to what is known as hysteresis, where the change in variables needed to push the system over a threshold differs between the two domains of attraction, being far greater when in the alternate (post-threshold) state (Folke et al. 2004). Hysteresis is a common phenomenon in coral reef ecosystems (Mumby, 2009; Hughes et al. 2010). For example, when urchin numbers returned to their previous, pre-threshold abundance the coral cover did not return due to other variables having been modified (Mumby et al. 2007). Thus, the required quantity of a previously important variable needed to maintain a certain state can differ considerably once the system has transitioned (Folke et al. 2004).

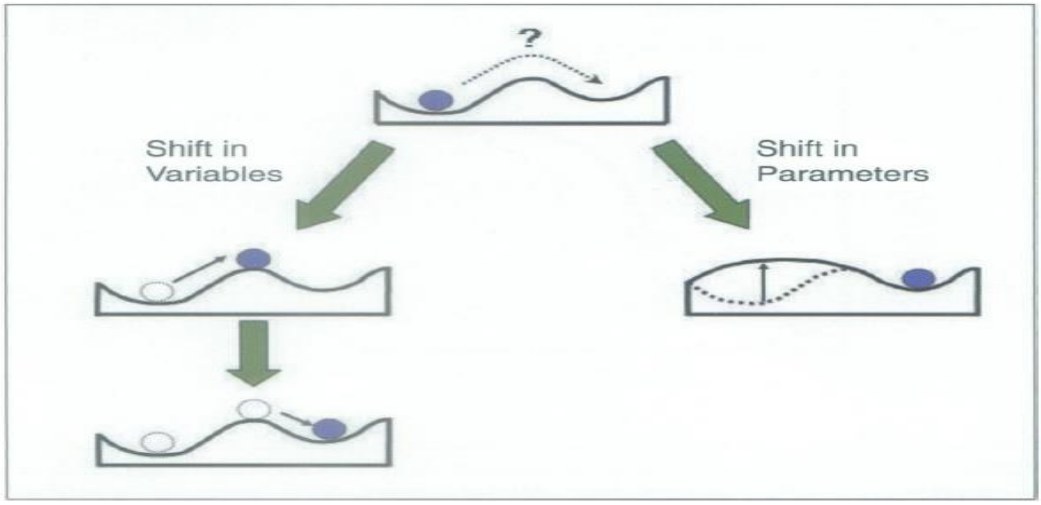

Fig. 1.2: Multiple stable states cup and ball model heuristic. The cups (troughs) represent the possible stable states or "basin of attraction". The balls represent the possible state of the system at a single time. Reproduced from Beisner et al. (2003).

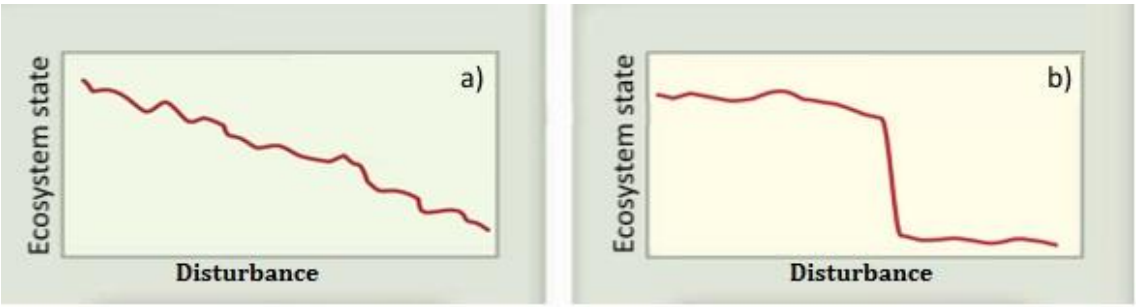

Fig. 1.3: Theoretical responses to of an ecosystem's state to disturbance: a) a linear decline in ecosystem state; and b) a state that initially exhibits resistance to disturbance before passing a threshold, after which an abrupt change in ecosystem state is seen. Reproduced and adapted from Scheffer et al. (2012).

1.3.1.2. Engineering resilience

Another prominent definition of resilience in an ecological context, as originally described by Pimm (1984), states that resilience is the time taken for a system to return to its normal levels of functionality after a disturbance (Pimm, 1984; Wang and Blackmore, 2009; Müller et al. 2016). However, this has been slightly extended to the degree to which an ecosystem state or property can resist or recover from disturbance (Oliver et al. 2015). This definition is sometimes cited as engineering resilience (Standish et al. 2014), which is what it will be referred to as the remainder of this thesis.

Adapted from the eponymous field of study, the main assumption of engineering resilience is that after a disturbance an ecosystem will return to its pre-disturbance state as it is near a stable equilibrium (Pimm, 1984; Holling, 1996a). This can be conceptualised in graph form, whereby the three distinct aspects of engineering resilience

can be assessed individually: resistance, persistence and recovery (Hodgson et al. 2015; Nimmo et al. 2015).

Resistance is measured as the resulting change in an ecological state caused by a disturbance, whereas recovery is the time after which the ecological state has returned to its pre-disturbance value (Grimm and Wissel, 1997; Liao, 2012; Bartels et al. 2016) (Fig. 1.4). Persistence relates to the extent to which an ecosystem or community continues over time after being perturbed (Grimm and Wissel, 1997; Donohue et al. 2016), allowing determination of whether there has been a net change (Nimmo et al. 2015). In this way, persistence could be measured as the difference between a pre-disturbance value and its final value after an allotted amount of time (Nimmo et al. 2015; Donohue et al. 2016).

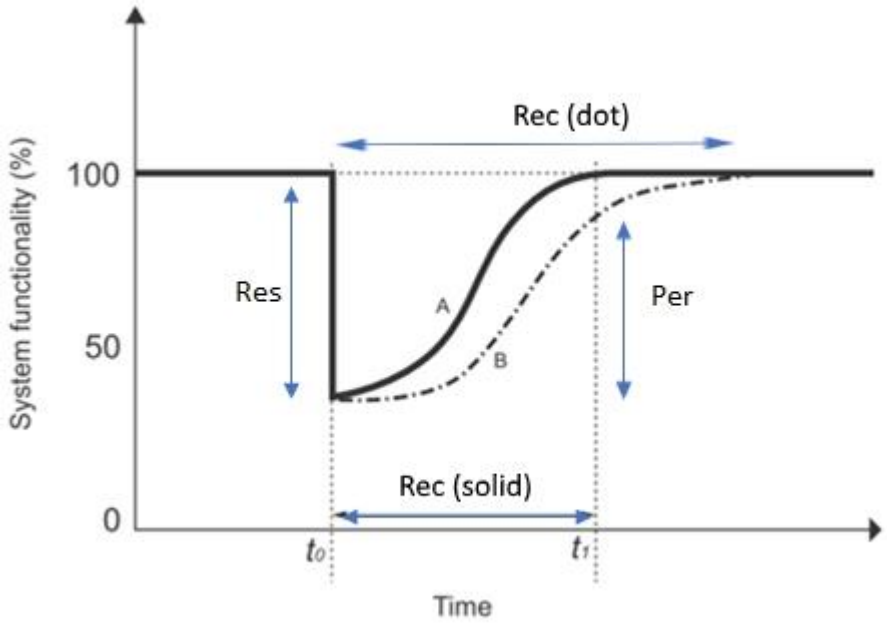

Fig. 1.4: Representation of engineering resilience. The solid black vertical line at *t0* represents the resistance (Res) of the conceptual system. The time taken for system A (solid black line) to recover fully (i.e. reach 100% of system functionality) is defined by the time between *t0* and *t1* (Rec (solid)). The recovery time of B (dotted black line) would be where the dotted line reaches 100% system functionality (Rec (dot)). The persistence of system B at *t1* is represented by the blue vertical arrow on the right (Per). Adapted from Liao (2012).

Resistance, persistence and recovery provide uncomplicated, interpretable and operationally-viable metrics of resilience (Nimmo et al. 2015; Donohue et al. 2016), making engineering resilience simpler to measure than ecological resilience (Liao, 2012; Nimmo et al. 2015; Donohue et al. 2016). Furthermore, resilience in this context can be measured as absolute (e.g. species richness change) and proportional values (e.g. percentage of unique species lost) (Nimmo et al. 2015). However, for a comprehensive

assessment, prior conditions need to be met to be able to calculate engineering resilience, the main one of which is that pre-disturbance baseline data needs to be known (Müller et al. 2016). This is needed as engineering resilience is measured in relation to pre-disturbance values.

Table 1.1: Summary of the two types of resilience used in an ecological context.

	Ecological resilience	**Engineering resilience**
Main assumption	Multiple stable states exist.	An ecosystem will return to its pre-disturbance state after a disturbance.
Focus	Existence of current functionality	Efficiency of current functionality
Measurement	Magnitude of disturbance that can be absorbed before transition to another state (i.e. proximity to thresholds)	Resistance to disturbance, time taken to recover to pre-disturbance state and persistence when undergoing disturbance.
References	Holling,1973; Holling, 1996a,b; Walker et al. 2004; Standish et al. 2014	Pimm, 1984; Holling, 1996a,b; Nimmo et al. 2015; Donohue et al. 2016

1.3.2. Applying the resilience concepts

As described by Holling (1996) and others (e.g. Walker et al. 2004), the two definitions of resilience focus on slightly different aspects. The first (ecological resilience) pertains to the *existence* of the ecology unit, whereas the other (engineering resilience) focuses on the *efficiency* of the ecology unit. Nonetheless, these aspects are related. For instance, when applying the engineering resilience concept, an ecological state that never recovers after a disturbance could be assumed to have entered an alternate stable state (Shade et al. 2012; Müller et al. 2016). Additionally, an ecosystem could be interpreted to have changed states as a relatively immediate effect of a disturbance, while at larger spatial and temporal scales this is part of the overall recovery process (Turner, 1990; Scheffer and Carpenter, 2003; Peters et al. 2007). Therefore, to provide measurements of resilience as to be useful for management, it is suggested that gaining a comprehensive understanding of resilience at all scales requires both definitions of ecological and engineering resilience to be considered, together with their operational limits of application (Walker et al. 2004; Standish et al. 2014). Specifically, the threshold concept from ecological resilience and the calculations of resistance, persistence and recovery from the engineering resilience definition should be included for a full assessment of

resilience for management and policy (Walker et al. 2004; Standish et al. 2014; Nimmo et al. 2015; Bartels et al. 2016; Donohue et al. 2016).

1.3.3. Resilience of what?

Resilience literature in ecology is largely theoretical, especially when the focus is on ecological resilience rather than engineering resilience. Consequently, ecological resilience concepts, including thresholds, normally relate to stable states of an ecosystem, as described in 1.3.1.1. Such states may include those of woodland, defined by a certain level of canopy cover (Staver et al. 2011), or a specific community present in an aquatic system (Jackson et al. 2001; Hughes et al. 2010). In this context, it is generally pre-threshold resilience that is important – resilience that maintains a state in a desired condition, thus stopping transition to an undesirable state (Standish et al. 2014).

However, the desirability of resilience does not always pertain to a stable state, but rather specific variables within a state (Nimmo et al. 2015). For example, a conservationist may only be interested in the abundance of species of conservation concern, while others may be purely interested in carbon sequestration or productivity. Therefore, desirable resilient aims may differ between organisations or people (Standish et al. 2014), and different conclusions could be drawn from the same study. This is emphasised in studies such as that of Reemts and Hansen (2007), where 65 transects of moderately or severely burned oak stands were recorded eight times over 11 years after a fire. The study found that although the woodland state (i.e. a dense tree area) returned within 10 years, the composition was different; oak (*Quercus* sp.) remained largely dominant but a locally important species, Ashe juniper (*Juniperus ashei*), was significantly less abundant, which meant that golden-cheeked warblers (*Dendroica chrysoparia*) declined by 80% in those burnt areas. Thus, although the woodland state recovered, the state variables of juniper and the warblers did not. It is for this reason that specific variables of interest should be defined and made explicit before resilience measurements, to reduce further confusion regarding resilience in research or management (Brand and Jax, 2007; Cumming, 2011).

For the above reasons, any study focused on resilience should specify beforehand what ecosystem state, property or phenomenon is being considered is required - i.e. what is the subject of assessment, what is desirable to be resilient (Carpenter et al. 2001; Zavaleta and Chapin, 2010; Allen et al. 2016; Bartels et al. 2016)? This is important in determining what specific measurements will need to be taken to fulfil aims (Nimmo et al. 2015).

1.3.4. Resilience to what?

For both ecological and engineering resilience, resilience of an ecosystem is based on a system's reaction to specific disturbance (Suding and Hobbs, 2009; Standish et al. 2014; Hodgson et al. 2015; Bartels et al. 2016). Therefore, it is important to determine what disturbance resilience will be measured in respect to, as different disturbances may produce disparate outcomes (Carpenter et al. 2001; Allen et al. 2016). This can correspond to specific disturbance regimes, which include the frequency and intensity of any disturbance (Pickett and White, 1985). However, in real-life this is difficult to define precisely for various reasons: i) the same disturbance can have varying impacts on different systems at the same time, or on the same system at different times; ii) disturbances can impact terrestrial ecosystems at varying scales (Pickett and White, 1985; Peterson et al. 1998; Turner, 2010); iii) the properties of disturbance are variable (Donohue et al. 2016); and iv) resilience is contingent on the collective behaviours of disturbances, not necessarily a single disturbance (Seidl et al. 2014a). To overcome these difficulties, specific disturbances need to be defined in any research beforehand, together with acknowledgment of the uncertainty of disturbance (Carpenter et al. 2001; Bartels et al. 2016).

1.3.5. Resilience at the landscape scale

Another decisive factor of resilience is the spatial scale used to assess it (Carpenter et al. 2001; Standish et al. 2014; Hodgson et al. 2015; Nimmo et al. 2015; Allen et al. 2016). This is owing to disturbances, biodiversity and ecosystem processes operating at different scales that influence the mechanisms and feedbacks responsible for making a system resilient (Peters et al. 1998; Heffernan et al. 2014; Peringer et al. 2016; Fig 1.5) and due to the patterns created as a response of historic processes (Kauffman, 1993). For example, in a forested landscape: at the plant scale, predominant fast biophysical processes control plant physiology; at the larger stand scale, interspecific plant competition for nutrients, light, and water influences species composition, tree growth and regeneration (Uhl et al. 1988; Rentch et al. 2010; Flaver et al. 2014), which in turn creates unique niches for relatively small faunal assemblages; at forest scale, disturbances including fires, storms, pest and pathogen outbreaks, and ungulate herbivory influence forest succession dynamics and structure at different locations within the forest, and over varying temporal scales, from years to decades (Dale et al. 2001; Raffa et al. 2008); and at landscape scale, processes relating to climatic, geomorphologic, and biogeographic influences shape

structure of habitats and dynamics across hundreds of kilometres, and over hundreds of years to millennia (Peters et al. 1998; Dale et al. 2001; Fisichelli et al. 2014).

Of these scales, it is at the larger scales, particularly the landscape scale, that the study of resilience is in its infancy. This means that the complexity of cross-scale interactions explored above has rarely been assessed with respect to resilience. In addition, studies of landscape resilience are constrained due, in part, to two issues: a lack of an operational definition as to what landscape resilience means, and a difficulty in estimating or measuring it (Allen et al. 2016; Newton, 2016). The difficulties of defining and measuring landscape resilience stem from needing to ensure that all the effects of relationships between scales at which different system processes operate are incorporated, including the frequency and/or magnitude of their interactions. This has inhibited the application of landscape resilience to the real world, including studies of what may influence resilience at larger scales (Peters et al. 1998).

Currently, the few authors that have sought to define landscape resilience have largely adapted the definition from the ecological resilience definition, thus experiencing the same issues. For example, Cumming et al. (2013) defined landscape resilience as akin to a complex adaptive system that can deal with disturbances, is spatially located and includes interactions between ecological aspects and people; Barbosa and Asner (2017) determined it as the capacity of biota to reorganise to a pre-disturbance state; and DeRose and Long (2014) regarded it as the influence of a particular disturbance on future structure and composition of woodlands. However, Tambosi et al. (2014) stated that landscape resilience, in the context of ecological restoration, is the capacity of recovery of biota through immigration after local biodiversity losses, a definition that is more analogous to engineering resilience.

Even with a lack of guidance regarding its measurement, several frameworks have been created that have listed principles thought to enhance landscape resilience. Beller et al. (2015), for example, in the context of socioecological systems, separated seven major factors that are each thought to contribute in a different way to landscape resilience. These include: the constraints of a landscape; physical, chemical and biological processes occurring; connectivity, diversity and complexity; functional redundancy; overlapping functions that provide protection against loss of a single function; scale; and people. Biggs et al. (2012) highlighted similar principles in the context of management aiming to enhance landscape resilience, adding that slow variables and feedbacks need to be managed and that understanding, learning and experimentation are important to promoting resilience. Moreover, in a purely ecological and spatial context, Cumming

(2011) included variations in habitat loss, patch-surroundings, fragmentation of landscapes and spatial habitat composition as aspects that influence landscape resilience. There are several common themes within the landscape resilience frameworks described above, most of which pertained to landscape diversity and connectivity.

Landscape diversity refers to the key components of landscapes, which are the numerous different species and biophysical environment. Generally, there is consensus that landscape stability increases with spatial variation, as relationships across diverse landscapes are dynamic relating to structural, trophic and disturbance elements and their interactions (Peters et al. 1998; Cumming et al. 2011). Higher levels of biodiversity; functional redundancy, the amount of species in an ecosystem that contribute the same or a similar function (Laliberté et al. 2010), and disparate habitat patches have been proposed to enhance the overall resilience of the landscape, as dissimilar habitats and groups respond to disturbance differently (Debinski and Holt, 2000; Mori et al. 2013; Mouillot et al. 2013; Altieri et al. 2015; Oliver et al. 2015).

Landscape connectivity is perhaps the most widely regarded as being an aspirational influencing factor of landscape resilience (Standish et al. 2014; Tambosi et al. 2014; Oliver et al. 2015). This is due to higher degrees of connectivity being expected to be advantageous by influencing dispersal and establishment probability and therefore the turnover and recovery of species, maintaining beta diversity (Wang and Loreau, 2014). This has been observed in abandoned field recolonisation and dispersal studies, in which greater connectivity enabled quicker recolonisation and dispersal (Standish et al. 2007; Oliver et al. 2013; Jakobsson et al. 2016). However, seemingly contrary conclusions have been drawn from other research that claims highly connected landscapes could lead to propagation of disturbances and therefore result in lower resilience (Loreau et al. 2003; Rahel, 2007; Gonzalez et al. 2009). This has been theorised in the context of homogenous landscapes including monoculture agricultural and wooded landscapes (Saab et al. 2014), where pest outbreaks have devastated a high proportion of the land cover, only slowing when its food source (i.e. the plant species) populations dwindle (USDA, 2012). In such examples, a more broken and less connected landscape may have increased resilience (van Nes and Scheffer, 2005; Biggs et al. 2012; Altieri et al. 2015).

As a result of landscape connectivity being seen as influential for enhancing resilience, the notion that connectivity infers resilience has been accepted by policy and management, where aims to increase the connectivity of natural systems have been incorporated into resilience strategies (e.g. Heller and Zavaleta, 2009; Lawton et al. 2010;

JNCC, 2012). Like resilience, however, difficulty exists when defining connectivity owing to the array of ways there are of quantifying it (Goodwin, 2003), possibly leading to further misuse of both concepts.

In ecology, connectivity is defined, broadly, as the capacity of landscapes to facilitate flow of organisms and ecological processes (Taylor et al. 1993; Tambosi et al. 2014), and generally relates to one of two components: structural or functional connectivity. Structural connectivity refers to the habitat pattern of landscapes and is measured using metrics of landscape composition and configuration, as these describe landscape heterogeneity and structure. Such metrics include total habitat area, isolation and edges of habitat (Estreguil et al. 2013; Haddad et al. 2015). Functional connectivity is more complicated and incorporates metrics pertaining to the capacity, facilitation and flows of ES and biodiversity (Tambosi et al. 2014), dispersal success and probability of movement (Goodwin, 2003; Estreguil et al. 2013), and proximity of patches, matrix permeability, and (re)colonisation dynamics (Tambosi et al. 2014).

To be able to apply the concept of landscape resilience in practice and therefore justify its use as a measure in policy and management, appropriate guidance is needed. Such guidance needs to be informed by empirical studies and should determine what effect factors that are hypothesised to enhance landscape resilience, such as certain metrics of connectivity, have with respect to likely disturbances, if any. Although the few definitions that exist of landscape resilience generally view the landscapes in terms similar to ecological resilience, the use of engineering resilience measurements would provide a more informative and robust way of assessing landscape resilience due to the defined metrics (Donohue et al. 2016; Nimmo et al. 2015).

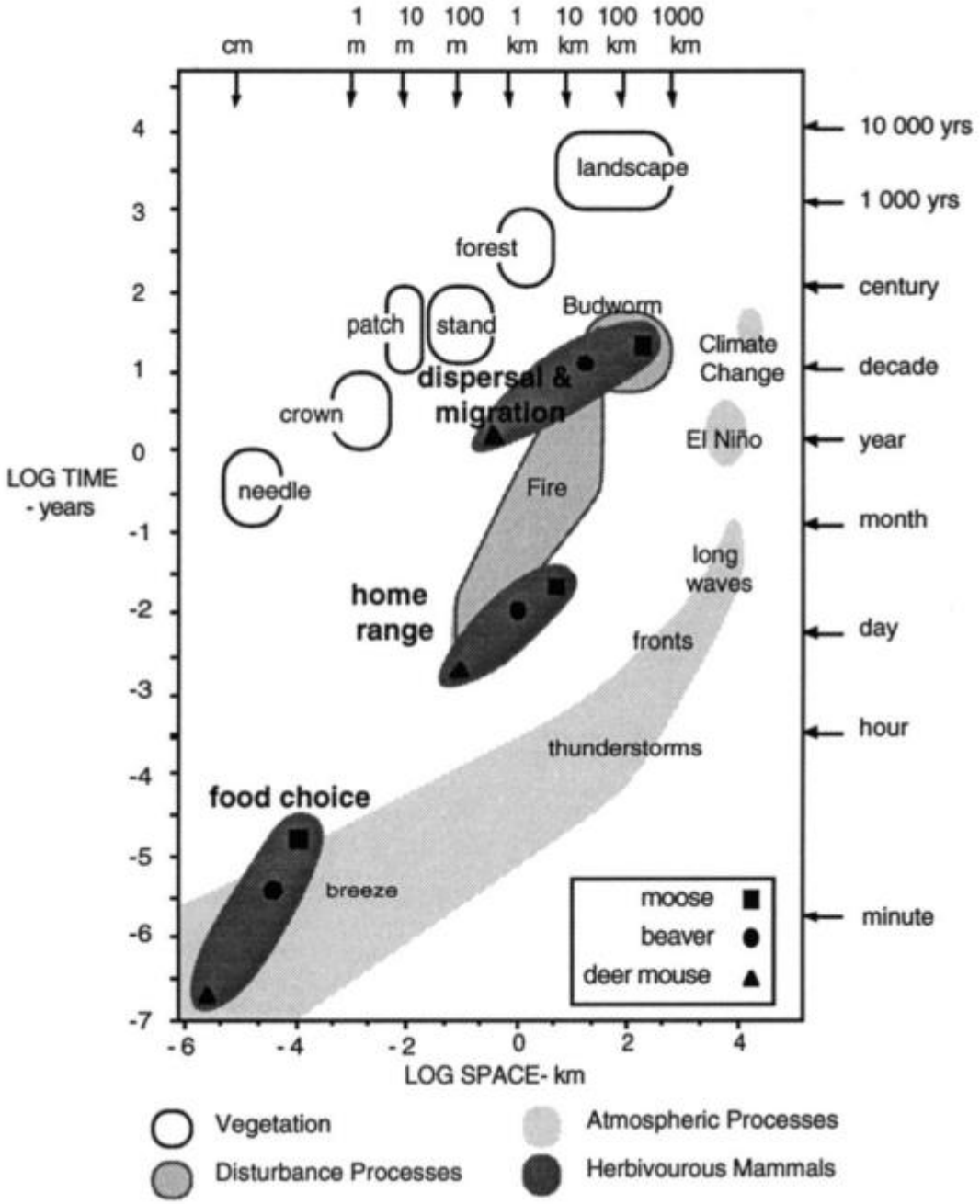

Fig. 1.5: Representation of the processes that structure forests over different temporal and spatial scales. The different black symbols represent the variations of actions of herbivorous mammals based on body size, with squares, circles and triangles representing mammals the size of moose, beavers and mice, respectively. Reproduced from Peters et al. (1998).

1.3.6. Resilience assessments and indicators

The ultimate reason for studying resilience and including it in policy is to identify risks and opportunities, prevent the loss and decline of important aspects of natural systems (e.g. biodiversity or ES) and, if required, identify alternative management strategies (Quinlan et al. 2016). Failure to implement the right strategy could result in the irreversible decline of the important products of an ecosystem. For example, misinformed

strategies have previously led to the loss of livestock production in rangelands (Ellis and Swift, 1988; Buttolph et al. 2004) and collapse of fisheries (Nayak et al. 2014).

Even when it is not possible to avoid severe degradation of an ecosystem, studies on resilience can still inform management policies that contribute towards conserving some important aspects of that ecosystem (Lindenmayer et al. 2016). Consequently, there is a growing demand to develop metrics that can be used operationally in the measurement of resilience (Bennett et al. 2005; Quinlan et al. 2016). However, there are considerable challenges to devising appropriate and useful metrics for this, owing to the complex ecological systems in which resilience cannot be easily determined (Quinlan et al. 2016).

To counter some of the challenges, resilience assessments, rather than the actual measurement of resilience, have been utilised in management systems to enable greater understanding of the current system dynamics at a given location and time (Bennett et al. 2005; Walker and Salt, 2012; Quinlan et al. 2016). Resilience assessments do not monitor and measure resilience directly, but rather use surrogates or proxy measures as indicators to infer how resilient a system is by using knowledge about the system of interest (Bennett et al. 2005; Carpenter et al. 2005; Scheffer et al. 2015; Quinlan et al. 2016). Indicators are surrogates for overall condition or response of an ecosystem when all individual factors are too difficult to assess (Hyman and Leibowitz, 2001; Turnhout et al. 2007). In effect, they are the canary in the mine used to determine changing environmental conditions (Burrell and Siebert, 1916). In ecology, a vast array of indicators has been developed for summarising broad trends at different scales (Noss, 1999; Niemi and McDonald, 2004; Gao et al. 2015). For example, lichen have been used as an ecological indicator of air quality (Sett and Kundu, 2016), and land cover and its change have been used as a proxy for ES provisions (e.g. Koschke et al. 2012). The UK uses broad taxa indicators to determine wider changes in overall biodiversity, to help fulfil its commitment to the Convention on Biological Diversity and avoid biodiversity loss (JNCC, 2012). For forest ecosystems specifically, indicators often provide proxy measures for the three main attributes of forest condition, namely composition, structure and function (Noss, 1999; Newton, 2007; Gao et al. 2015), while other useful indicators provide proxy measures for whole stand development, growth and regeneration (Trumbore et al. 2015). Therefore, a rich wealth of knowledge regarding possible indicators is available.

However, resilience assessments differ in two important ways from ecological indicators, all of which need to be considered when deciding whether an indicator may be appropriate (Carpenter et al. 2001; Bennett et al. 2005). First, resilience depends on

scale, whereas ecological indicators may not (Carpenter et al. 2001). Second, indicators may only address the state of an ecosystem property at the current time, whereas resilience is a measurement over time (Carpenter et al. 2001; Scheffer et al. 2015). To overcome these differences, proposed indicators should focus on slow-changing variables when testing indicators for resilience – i.e. ones that change monotonically over time with condition (Carpenter et al. 2001; Bennett et al. 2005; Walker et al. 2012; Nemec et al. 2014). Slow-changing variables are often the controlling variables, which will ultimately affect the fast-changing variables. Thus, while the fast-changing variables, such as a species or ES, may show more variation in the short term, the slow-changing ones will ultimately determine the level of resilience in a known system (Walker et al. 2012). Resilience assessments of slow-changing measures have previously included nutrients in sediment and soil in lake districts, while in more socio-ecological systems, leasehold arrangements and other social input may have to be considered in addition to changing ecological variables, as both could result in major changes over time (Carpenter et al. 2001; Quinlan et al. 2016).

Ideally, surrogate indicators that are used to infer resilience should be initially collected over a gradient of environmental change, with observations performed at discrete levels if possible (Scheffer et al. 2015). Such a measure enables a greater wealth of knowledge of the complex properties of that particular ecosystem to be obtained, which in theory lessens the inaccuracy of any subsequent resilience assessments (Scheffer et al. 2015). Such indicators need to be clearly defined, scale-relevant and measurable with regard to the wealth of, or lack of, previous data pertaining to that particular location (Carpenter et al. 2001; Washington-Allen et al. 2008; Standish et al. 2014; Scheffer et al. 2015). Currently, in the context of using suitable indicators to assess resilience, effective indicators are lacking for most ecosystems (Carpenter et al. 2001; Oliver et al. 2015; Scheffer et al. 2015), and therefore more Surrogate indicators need to be discovered.

1.4. Knowledge Gaps

In a highly influential report, Lawton et al. (2010) examined the resilience of the UK's current environmental networks. The report concluded that England's wildlife sites were not resilient enough to deal with existing threats, let alone future pressures such as climate change. In response to the issues raised in Lawton et al. (2010) and NEA (2011), the first Natural Environment White Paper (NEWP) in 20 years was published (HM Government, 2011). The NEWP specifically identified that the UK woodlands and their services are essential to maintain, for both the conservation of British wildlife and valuable amenities to support human well-being (i.e. ES) (HM Government, 2011). The NEWP therefore committed to providing "appropriate protection to ancient woodlands" (HM Government, 2011, p69), conceding that "forests and woodlands must play a full part in achieving a resilient ecological network across England" (HM Government, 2011, p25). However, there are some significant knowledge gaps involved with being able to incorporate resilience concepts in an effective way, largely owing to resilience being theoretical and thus lacking empirical evidence especially in temperate landscapes (Standish et al. 2014; Newton, 2016).

Achieving such ambitious goals as those set out in the NEWP is difficult with the current ambiguity and lack of quantification regarding resilience. Therefore, to gain knowledge about how resilient woodlands are and what factors may influence resilience in the future, there are crucial steps that need to be taken. The first is to discover how important underlying properties of woodlands such as biodiversity, ecosystem functions and ecosystem services change as woodlands undergo degradation (Groffman et al. 2006; Carpenter et al. 2009). This includes testing whether there are points at which a small change in environmental conditions could lead to an abrupt change in important woodland EPs (Muradian, 2001; Lindenmayer and Luck, 2005; Steffen et al. 2015).

Like many ecological processes, little progress has been made in extrapolating stand level resilience and dynamics to the landscape scales (Peters et al. 1998; Oliver et al. 2015). Therefore, the second step involves elucidating what the main factors influencing resilience at the landscape scale are based on the dynamic changes of EPs at smaller scales (Lambin and Meyfroidt, 2011; HM Government, 2011; Tambosi et al. 2014; Oliver et al. 2015).

Using obtained knowledge of resilience of important EPs at the different scales, managers, researchers and policymakers will be better enabled to produce sufficient plans to help manage for more resilient woodlands in the future. However, such information needs to be combined with a way of determining localised resilience in the field so that it

can be fed into adaptive management plans effectively (Bennett et al. 2005; Quinlan et al. 2016). Therefore, to meet this need suitable surrogate indicators need to be elucidated so that they can be used in future resilience assessments (Carpenter et al. 2001; Scheffer et al. 2015; Quinlan et al. 2016). This may be able to be carried out through current cost-effective monitoring tools which are used to determine the condition of forest stands. Once knowledge regarding forest resilience has been obtained, it can be used in management and policy to aid the conservation of forests through enhancement of resilience.

1.5. Thesis focus, objectives and structure

1.5.1. Thesis focus

This research will examine a forest ecosystem in the UK that is currently undergoing dieback, as a result of the interaction of multiple stressors (Newton et al. 2011; Martin et al. 2015), to gain insight into the resilience of its woodlands. Specifically, four metrics of resilience will be considered in this work: i) the possibility of thresholds at the stand scale; and landscape scale ii) resistance; iii) persistence; and iv) recovery. In addition, changes associated with beech dieback will be measured in a woodland ecosystem to see if such measurements can be used as surrogates to infer the current resilience of woodland stands through resilience assessments.

1.5.2. Aims and objectives

The aims of this research are: i) to increase understanding concerning ecological thresholds, relating specifically to the biodiversity, and ecosystem services, functions and conditions of a forest ecosystem; ii) to determine how resilient forest ecosystem properties are at a landscape-scale; and iii) to determine the effectiveness of potential tools that could be used to infer dieback-related woodland condition, to provide insight into the usefulness of such tools in determining resilience.

The main question:

How resilient are the temperate woodlands of the New Forest and what tools can be used to infer resilience?

The specific objectives and questions of this thesis are:

1. To test the threshold hypothesis over a woodland dieback gradient.
    a. How are biodiversity, ecosystem functions and condition affected in a forest undergoing dieback?

2. To examine the effectiveness of rapid condition assessment tools as a proxy use for inferring woodland resilience.
    a. Can airborne lidar-derived structural condition measures be used to predict the ecological condition of tree stands, biodiversity and ecosystem properties?
    b. How effective is the current condition assessment method at detecting changes between the stages of dieback?

3. To determine whether woodland cover relates to resilience of ecosystem properties at a landscape scale.
    a. Does the amount of initial woodland cover affect ecosystem resilience at the landscape scale?

1.5.3. Thesis structure	Question 1a: How are biodiversity, ecosystem function and condition affected in a forest undergoing dieback?	Hypotheses: Threshold responses will exist in measures of: 1) biodiversity 2) ecosystem function; and 3) ecosystem condition.
How resilient are the temperate woodlands of the New Forest and what tools can be used to infer resilience?	Question 2a: Can airborne lidar-derived structural condition measures be used to predict the ecological condition of tree stands, biodiversity and ecosystem properties?	Hypotheses: Field-measured variables of 1) biodiversity; 2) stand condition; 3) herbivore damage; and 4) soil condition will be able to be predicted by lidar-derived structural measures.
	Question 2b: How effective is the current condition assessment method at detecting changes between the stages of dieback?	Hypotheses: 1) Common Standards Monitoring (CSM) condition assessment results will vary significantly over a gradient of environmentally-induced dieback. 2) Non-CSM indicators could be used to effectively determine different beech dieback stages.
	Question 3a: Does the amount of initial woodland cover affect ecosystem resilience at the landscape scale?	Hypothesis: 1) Initial woodland cover influences landscape resilience under different disturbance intensities.

1.6. Study area: The New Forest, Hampshire

The study area that was used for the entirety of this thesis, the New Forest, was established as a hunting forest in the 11th century by William the Conqueror (Tubbs, 2001), and is of exceptional importance for biodiversity conservation (Newton, 2010). A brief description of the New Forest is provided here as context for the following chapters of this thesis.

The New Forest is positioned mainly in the county of Hampshire on the south coast of England (longitude: 1˚17'59'' to 1˚48'8'' W, Latitude: 50˚42'19'' to 51˚0'17'' N) and its official boundaries, known as the perambulation of the Forest, encompass close to 38,000 hectares, with a small percentage in private ownership (Berlin et al. 1960; Newton, 2010). In 2005, the New Forest National Park (NP) was created. The NP encompasses a larger area of approximately 57,000 ha, and includes the perambulation within its boundaries (Chatters, 2006). The New Forest also has many other conservation designations, including 20 Sites of Special Scientific Interest (SSSIs), two Ramsar Convention sites and six Natura 2000 sites (Newton, 2010). The local climate is oceanic and temperate, with a mean annual maximum temperature of 14.8˚C and annual rainfall of 835.2 mm, based on data available between 1981 and 2010 (Met Office, 2015).

The New Forest is underlain by soft, sedimentary clay and sandy soils of Tertiary age deposited during the Palaeocene. It lies in the centre of the Hampshire Basin, a chalk syncline (Tubbs, 2001). The New Forest's core extends across a marginally elevated plateau that slopes gently from north to south at between 1˚ - 2˚, with deeper valleys in the north. Another important aspect of the New Forest's geology is that the landscape is dominated by gravel terraces, which derive from the time that the New Forest used to be either a sea or estuary. Overall, the New Forest is a mixture of base-poor acidic soils, with flat, gravelly areas; well-drained clay and loam; and marshy bogs and mires, which continuously are waterlogged (Tubbs, 2001).

Together with its geology, free-roaming large herbivores in the New Forest have helped shape the character of the Forest since medieval times through influencing the structure of the wood and impacting regeneration. High densities of ungulates, which include livestock and deer (Newton, 2010), still roam freely in the modern day, partly owing to the unique commoning rights of the Forest's human inhabitants.

Resulting from its unique history, the New Forest features three habitats that are rare and highly fragmented in lowland Britain: heathland, valley mire and ancient pasture woodland. When combined, the areas of these habitats form the main area of the New Forest Special Area of Conservation (SAC), which altogether spans approximately 29,213 ha (JNCC, 2011) (Fig 1.6) and supports an exceptional array of biodiversity.

Twenty-nine per cent of the SAC designation is classified as broadleaved deciduous woodland, claiming the 'most extensive area of active wood-pasture with old oak (*Quercus* spp) and beech (*Fagus sylvatica*) in north-west Europe' (JNCC, 2011) at approximately 5,000 ha (Chatters, 2006). The ancient woodland, coined the Ancient and Ornamental (A&O) woodlands in the New Forest Act 1877, is covered by the SAC, and provides the greatest area of semi-natural vegetation in lowland Britain (Tubbs, 2001). Beech and oak dominate the SAC woodland habitats, with abundant holly (*Ilex aquifolium*) in the shrub layer. The structure of the woodlands is variable and dynamic, including veteran trees that originated as far back as the 17th century, ancient woodland (i.e. wooded since 1600 AD), pasture-woods, open areas with a high quantity of lying dead wood and standing dead wood, and new woodland expansion. The SAC encompasses all the individual sites of the New Forest that were used in this thesis.

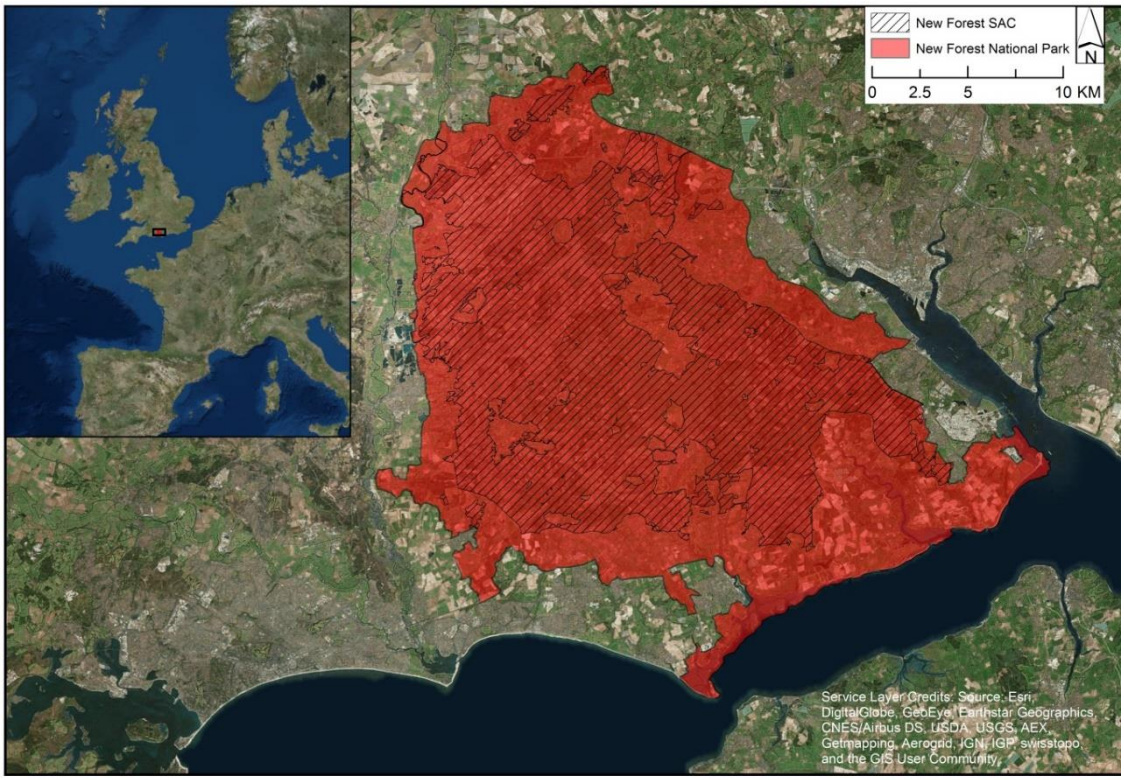

Fig. 1.6: The extent of the New Forest Special Area of Conservation (SAC; hatched) and the New Forest National Park (red).

1.6.1. Beech dieback in the New Forest

Beech trees have experienced high mortality rates in the New Forest over the last few decades, the determinate causes of which are uncertain (Tubbs, 2001; Newton, 2010). A major drought that occurred in 1976 is hypothesised to be one of the main contributing factors. This is based on data from Denny Wood, a section of the New Forest that has

been recorded for the past 50 years (Manners and Edwards, 1986; Mountford et al. 1999; Mountford and Peterken, 2003; Martin et al. 2015). The 1976 drought is similarly thought to have killed many large beech trees in other parts of the UK, such as Lady Park Wood in the west of England, in which large-scale beech mortality continued for 15 years after the drought (Peterken and Mountford, 1996). In addition, historically strong storms in 1987 and 1990 are also thought to have contributed to large beech tree mortality trends (Mountford et al. 1999; Mountford and Peterken, 2003), while debarking by grey squirrels and self-thinning affect smaller-stemmed beech trees (Mountford and Peterken, 2003; Mountford et al. 1999).

Martin et al. (2015) showed that beech mortality is still ongoing in the New Forest, with sections of Denny Wood declining by a mean of 32% basal area (BA) over 50 years. The study suggested that continued climate change and associated growing season temperatures could have led to serious water deficits since 1976, contributing to the large scale dieback of beech (Martin et al. 2015). Similar increased summer temperatures and water deficits are thought to have caused beech dieback throughout Europe (Zimmermann et al. 2015; Cavin and Jump, 2016).

Water deficits can majorly affect beech, as it is a highly drought sensitive species (Packham et al. 2012). The shallow roots of beech may limit the water exploitation potential of beech (Peterken and Mountford, 1996). Under drought conditions, when beech has a limited ability to take up water, its xylem potential drops swiftly (Scharnweber et al. 2011). Additionally, when stressed, beech appears to be unable to exploit wetter soils by expanding its root system (Lang et al. 2010), and has a high turnover of fine roots (Meir and Leuschner, 2008).

Other drivers of widespread beech dieback may become more prominent in the UK in the future as the climate continues to change. In mainland Europe and the USA the occurrence of *Phytophthora* fungi has become widespread and caused tree death to an extent in which it's too hard to manage (Jung et al. 2006; Jung, 2009; Cunniffe et al. 2016). The *Phytophthora* genus, which literally translates as 'plant destroyer' in Greek (Brasier, 2008), is a pathogenic fungus that causes mass damage to tree species worldwide. Recently, *Phytophthora ramorum* has been recorded in the New Forest, with beech being considered to be the most vulnerable species to the pathogen (Forestry Commission England, 2015). Therefore, the spread of pathogens and climate change are likely to be a combined threat in the future (Jung, 2009; Martin et al. 2015).

Chapter 2:
Thresholds of biodiversity and ecosystem function in a forest ecosystem undergoing dieback

2.1. Abstract

Ecological thresholds, which represent points of rapid change in ecological properties, are of major scientific and societal concern. However, very little research has focused on empirically testing the occurrence of thresholds in terrestrial ecosystems. To address this knowledge gap, it was tested whether a number of biodiversity, ecosystem functions and ecosystem condition metrics exhibited thresholds in response to a gradient of forest dieback, measured as basal area decline of living trees. The gradient of dieback was sampled using 12 replicate study areas in a temperate forest ecosystem. Our results provide novel evidence of several thresholds in biodiversity, namely species richness of ectomycorrhizal fungi, epiphytic lichen and ground flora; for ecological condition (e.g. sward height, palatable seedling abundance) and a single threshold for ecosystem function (i.e. soil respiration rate). Mechanisms for these thresholds are explored. As climate-induced forest dieback is increasing worldwide, both in scale and speed, these results imply that threshold responses may become increasingly widespread.

2.2. Introduction

The living world is currently experiencing an unprecedented period of environmental change (Rockstrom et al. 2009; Grimm et al. 2013; Mace et al. 2014; Steffen et al. 2015). In recent decades, human-derived actions such as carbon emission, movement of species and large-scale land transformations (e.g. urban and agricultural expansion) have become pervasive throughout the biosphere. Impacts of human activity have become so widespread and intrusive that a new geological epoch, the Anthropocene, has been proposed (Steffen et al. 2015). Human actions have influenced the functioning of the Earth system to such an extent that the consequences could be detrimental or even catastrophic for human society (Rockstrom et al. 2009; Grimm et al. 2013; Mace et al. 2014; Steffen et al. 2015). This is reflected in development of the planetary boundaries concept, which suggests that if specific thresholds of environmental change are transgressed, there may be increased risks to human wellbeing or to resilience of the whole Earth system (Rockstrom et al. 2009; Steffen et al. 2015).

The concept of planetary boundaries, together with allied concepts such as resilience (Rockstrom et al. 2009; Steffen et al. 2015), depends on the existence of

ecological thresholds. Such thresholds are defined as points or zones where relatively rapid change occurs from one ecological condition to another (Huggett et al. 2005), and are characterised by a non-linear response of an ecosystem property to a controlling variable that increases linearly (Scheffer et al. 2001). If thresholds occur in nature, a slight increase in disturbance intensity or frequency could cause a disproportionate change in an ecosystem property. Such changes could include the loss of biodiversity crucial for ecosystem function (Keith et al. 2013) and the loss of regulatory ecosystem services on which humans depend (MEA, 2005). Moreover, a threshold in one ecosystem property could sequentially disrupt the self-organising networks that govern local dynamics of other systems (Filotas et al. 2014), and could potentially cause unpredictable responses at the scale of whole Earth system dynamics (Huggett al. 2005; Anderies et al. 2013; Steffen et al. 2015). There is a need to avoid crossing such thresholds to enable ecological systems, and their associated socio-economic systems, to be maintained in the future (Farley and Voinov, 2016).

Ecological thresholds are thought to be attributable to shifts in the relative strength of balancing (i.e. negative) and reinforcing (i.e. positive) feedback loops that influence the dynamics of an ecosystem (Briske et al. 2010). For example, in many terrestrial ecosystems, low water availability acts to regulate the growth of plants. Conversely, if water availability increases by a sufficient amount, the biomass and complexity of vegetation can increase, which can further increase water availability by modifying the water cycle (Bonan, 2008; Sala and Maestre, 2014).

Despite the perceived global importance of ecological thresholds, supporting evidence is largely theoretical (Scheffer et al. 2001; Dakos et al. 2008), and the issue is the focus of major scientific debate (Barnosky et al. 2012; Brook et al. 2013). Supporting empirical evidence from field situations is severely limited (Radford and Bennett, 2004; Huggett et al. 2005), and is primarily available for aquatic systems (Jackson et al. 2001; Hoegh-Guldberg et al. 2007; Catalan et al. 2009). Field evidence for ecological thresholds resulting from environmental change is particularly lacking in terrestrial ecosystems (Huggett et al. 2005; Sasaki et al. 2015). This research therefore aimed to test the hypothesis that threshold responses exist in measures of 1) biodiversity, 2) ecosystem function and 3) ecosystem condition within a terrestrial ecosystem, specifically temperate forest. To test this hypothesis, a beech-dominated forest that is currently undergoing large-scale dieback in response to environmental change was examined, as revealed through analysis of long-term monitoring data (Martin et al. 2015).

2.3. Methods

2.3.1. Study area

We carried out this study in the New Forest National Park (NP), which covers an area of 57,100 ha situated in southern England (longitude: $1^0$17'59'' to $1^0$48'8'' W, Latitude: $50^0$42'19'' to $51^0$0'17'' N) (Fig. 2.1). The Forest consists of a mosaic of heathland, mire, grassland and coniferous and broadleaf woodland (8,472 ha) ecosystems, and includes the largest area of mature semi-natural beechwoods in Britain. The local climate is oceanic and temperate, with a mean annual maximum temperature of 14.8˚C and annual rainfall of 835.2 mm, based on data available between 1981 and 2010 (Met Office, 2015). The Park contains the largest area of semi-natural vegetation in lowland Britain (Tubbs, 2001), and is of exceptional importance for biodiversity conservation (Newton, 2010). The New Forest is also characterised by high densities of large herbivores, including livestock and deer, reflecting its history as a Royal hunting reserve (Tubbs, 2001).

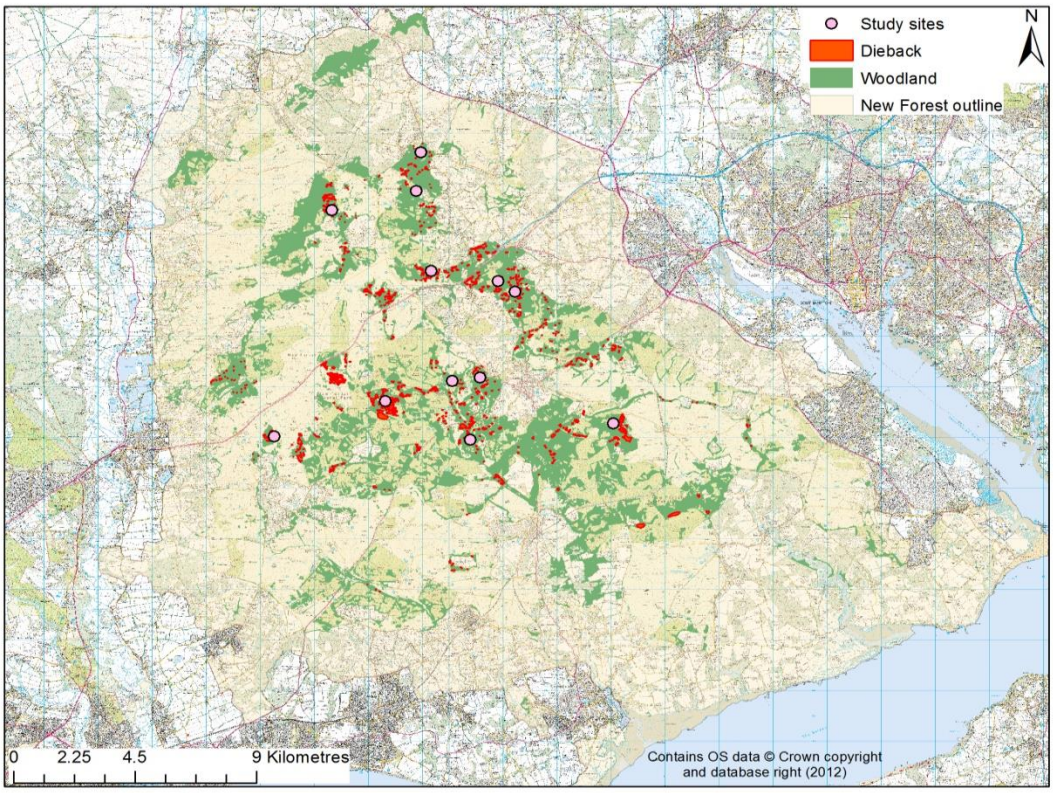

Fig. 2.1: Map of the New Forest National Park, Hampshire, UK. Green represents the areas of woodland and red represents the areas of dieback recorded in the Forest. The study sites for Chapter 2 are indicated by the pink dots.

2.3.2. Experimental design

A geographic information system (GIS) (ArcGIS 10.1) was utilised to identify suitable study sites of forest dieback within the New Forest. Spatial information included 25 cm

resolution aerial photographs, captured in 2007 by GeoPerspectives, and areas of known historic woodland dieback, recorded in 1999 (Peterken et al. 1999). The resulting areas of dieback were overlaid on top of several layers, including soil data (NATMAP; National Soil Map), obtained from National Soil Resources Institute (NSRI), Silsoe, Bedfordshire, UK; regeneration plots; and a tree composition map, derived from data collected in 1982 (Flowers and Tubbs, 1982). These were used to identify areas to ground-truth, based on the criteria of > 50% beech composition, no managed regeneration and soil homogeneity.

Study sites were chosen if it could encompass the five stages of the woodland dieback gradient and showed signs of dieback, such as dead beech trees. Overall, twelve replicates sites were used (Fig. 2.1). Within each site, five 20 x 20 m survey plots were established along a gradient of woodland dieback, using basal area (BA) as a measure of forest structure, calculated following Cantarello and Newton (2008).

To create a conceptualised gradient of forest dieback, the fundamental criterion was based on the stand BA of living *Fagus sylvatica* trees within each plot. Five stages were used: 1) intact (no dieback); 2) slight dieback; 3) moderate dieback; 4) major dieback; and 5) total dieback. The mean of the 12 intact plots was used as a baseline value. The other four plot stages were accordingly classified as slight dieback (25% BA less than the baseline value), moderate dieback (50% BA less), major dieback (75% BA less) and total dieback (100% BA less) (Fig. 2.2; Table 2.1). Other trees present in the plots, which were not included in the beech BA measurements, were mainly holly (*Ilex aquifolium*). Excluding the total dieback stage, holly made up < 22% total BA for all plots, with a maximum of 10.5 m^2 ha^{-1} BA for a single plot. In the total dieback plots, the highest BA of holly was 10.5 m^2 ha^{-1}.

Secondary criteria required canopy openness to increase as the stages of dieback increased, the total dieback stage being greater than 50% openness. Furthermore, it was required that plots that were dying back had standing or lying dead wood present; however, this was not a requirement for the intact stage plots, although dead wood could still be present.

The edges of each plot were delineated with measuring tapes. A compass was used to confirm that the adjacent angles were at 90˚ angles. A nested sub-plot of 10 x 10 m (100 m^2) was set up in the centre of each plot, laid out in the same orientation as the full plot. The centre and the corners of the sub-plot were marked with wooden stakes for easy identification on return visits. The mid-points of each plot were recorded using a handheld GPS (GPSMAP 60CSx; Garmin, USA). Due to the nature of the spatial dieback, plot

location was purposeful and not totally random, and the distribution of plots within a study site was not uniform.

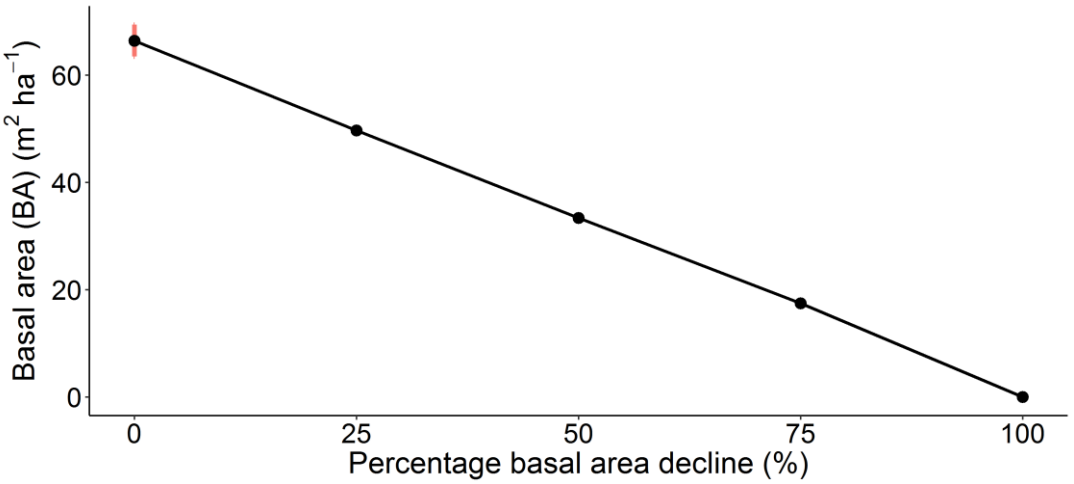

Fig. 2.2: The mean stand basal area (BA) of dieback stages of the gradient plots. Standard error bars are shown in red.

Table 2.1: Basal area (BA) statistics for each stage of dieback. Mean, standard deviation (SD), standard error (SE), confidence interval (CI), minimum (Min) size of BA and maximum (Max) size of BA for each of the stages of dieback.

		Basal area of beech (m^2 ha^{-1}; BA)					
Percent basal area decline	**n**	**Mean**	**SD**	**SE**	**CI**	**Min**	**Max**
0%	12	66.42	10.29	2.97	6.54	59.85	98.39
25%	12	49.71	1.36	0.39	0.86	47.73	52.12
50%	12	33.37	1.79	0.52	1.14	30.58	37.12
75%	12	17.45	1.47	0.42	0.93	13.65	19.44
100%	12	0	0	0	0	0	0

2.3.3. Field measurements

Within each survey plot, the tree species and diameter at breast height (DBH, 1.3 m) was recorded (see Appendix 2.1 for DBH measurement details). Detailed surveys of each plot were then undertaken to identify species of epiphytic lichens, ground flora, tree saplings and seedlings and ectomycorrhizal fungi (ECM) based on the identification of sporocarps. In five sites ground-dwelling arthropods were trapped in pitfall traps and identified using DNA barcoding methods (see Appendix 2.2).

As soil condition and structure are important to the productivity of the whole woodland ecosystem, soils were sampled within each plot then analysed bulk density, nitrate, ammonium, potentially mineralisable nitrogen, C, K, P, S, Ca, Mg, Na, Al, Mn, pH, electrical conductivity, organic matter, soil moisture, soil temperature and particle

size distribution using standard analytical procedures. In-situ nitrogen mineralisation and nitrification was recorded using a resin capsule (Unibest, Walla Walla, WA, USA), following DeLuca et al. (2013) (see Appendix 2.1 for more in-depth details of assessment).

Measurements were also recorded for tree crown condition (Eichhorn et al. 2010), canopy openness (Jennings et al. 1999) and dead wood volume following Newton (2007). As a metric of herbivory, dung counts (Jenkins and Manly, 2008), plant browsing (Bergström and Guillet, 2002; Gibson, 2002) scrub layer presence and condition (Reimoser et al. 1999) and sward height (Stewart et al. 2001) were recorded. Aboveground biomass and carbon storage were calculated following Jenkins et al. (2011), based on constants from look up tables for specific species and the mean DBH. Soil respiration rate was measured with a portable EGM-4 Environmental Gas Monitor CO_2 infrared gas analyser (IRGA) equipped with a closed system soil respiration chamber (PP Systems, Amesbury, MA, USA). See Appendix 2.1 for more in-depth details of assessments. For all the variables measured, see Appendix 2.3.

2.3.4. Data analysis

All measured variables were analysed in relation to the BA gradient, with the twelve sites treated as independent replicates. As BA was scaled linearly along the gradient, any departure from linearity provided potential evidence of a threshold response. Generalised linear mixed models (GLMMs) were used to analyse these responses. This was achieved by fitting the most parsimonious models (determined using AICc) of the relationships between percentage BA loss and the response variables, using other measured predictors as fixed effects and study area as a random effect. Count data (i.e. non-negative integers) were modelled using a Poisson error structure. For proportional and percentage data, a small non-zero value was added to avoid infinite logit transformed values (Warton and Hui, 2010). AICc values were calculated using the maximum likelihood value of the model (Burnham and Anderson, 2002). AICc values were determined using the MuMIn R package (Barton, 2014) and used to define the most parsimonious model, following an information theoretic approach (Burnham and Anderson, 2002). Performance of models was evaluated by calculating the marginal r^2, which describes the proportion of variance explained by the fixed effect alone (Nakagawa and Schielzeth, 2013). All analyses were performed in R 3.1.2. (R Development Core Team, 2011, http://www.R-project.org) using the lme4 (Bates et al. 2013) and ggplot2 (Wickham, 2009) packages for mixed models. A response variable was considered to show a threshold if it met three *a priori*

criteria relating to the most parsimonious model: 1) the model included a quadratic term; 2) its ΔAICc was ≥ 3 compared to the next closest model; and 3) its marginal r^2 value was > 0.15.

These criteria were defined *a priori*, before conducting the analysis, to ensure a degree of rigour and objectivity in the detection of threshold responses. It should be noted that the criteria were developed by myself, based on what is considered to be consistent with good practice, as described by Burnham and Anderson (2002) and Bolker et al. (2008).

2.4. Results

Overall, 86 variables were tested across the BA gradient. Over half (44/86) of the measured variables showed non-linear responses over the dieback gradient in this study, of which 13 exhibited thresholds according to the *a priori* criteria, pertaining to biodiversity, ecosystem function and ecological condition (see Appendix 2.4, Table A2.4 for additional results).

2.4.1. Biodiversity

The relationship between ground flora species richness and dieback was best predicted by a regression model including both a linear and quadratic term of BA loss and a dung predictor term for all ground flora (r^2 = 0.60, AICc = Δ5.37) (Fig. 2.3a) and ground flora not including woody species (r^2 = 0.66, ΔAICc = 6.24). The most parsimonious ECM species richness model exhibited a threshold, with a quadratic and linear term of BA loss (r^2 = 0.57, ΔAICc = 8.30) (Fig. 2.3b). In addition, total epiphytic lichen species richness exhibited a threshold response, with linear and quadratic terms of BA loss and a holly abundance term included in the most parsimonious model (r^2 = 0.44, ΔAICc = 19.1) (Fig. 2.3c), while lichen species richness on beech trees specifically also exhibited a threshold response (r^2 = 0.60, ΔAICc = 57.32), exhibited by having a quadratic and linear BA loss as its terms. Thresholds were not present in ground-dwelling arthropod richness, which was best represented by a linear BA term (r^2 = 0.26, ΔAICc = 2.41) (Fig. 2.3d) or tree seedling richness, which was also best represented by a single linear BA term (r^2 = 0.19, ΔAICc = 2.02).

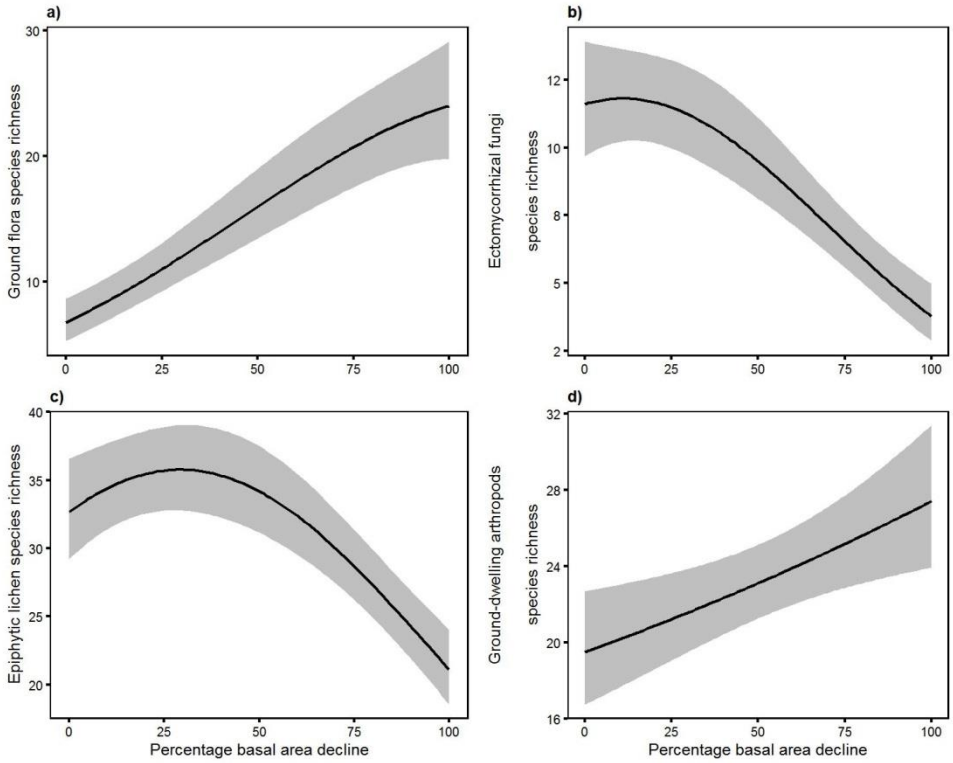

Fig. 2.3: Relationships between stage of dieback and species richness. Relationships between stage of dieback and species richness of a) vascular ground flora (n = 60); b) ectomycorrhizal fungi (n = 60); c) epiphytic lichen (n = 60); and d) ground-dwelling arthropods (n=25). The black lines represent prediction using the most parsimonious model coefficients and grey shading the 95% confidence intervals of the coefficients (marginal r^2 = 0.60, 0.57, 0.44, and 0.26 for a-d, respectively). All species richness values are the number of unique species found in 0.04 ha.

2.4.2. Ecosystem functions

Only a single threshold response was exhibited in the 27 soil function variables measured over the dieback gradient, namely the case of soil respiration rate, which demonstrated quadratic and linear terms of BA loss included in the most parsimonious model (r^2 = 0.16; ΔAICc = 3.71) (Fig. 2.4a). For other soil functions, models with non-linear terms were often the most parsimonious models; however, these displayed very low r^2 and ΔAICc values and were not therefore considered to be exhibiting thresholds. These included potentially mineralisable nitrogen in the mineral layer (r^2 = 0.07; ΔAICc = 0.53) (PMNM; Fig. 2.4b) and N mineralisation (r^2 = 0.13; ΔAICc = 0.97) (Fig. 2.4c). Other modelled soil function results indicated that strong linear relationships, but not thresholds, were exhibited in the exchangeable cations of Na (r^2 = 0.34; ΔAICc = 7.06) and Ca (r^2 = 0.18; ΔAICc = 3.91). Total carbon storage was best predicted by a model with solely a linear BA term (r^2 = 0.50; ΔAICc = 1.14) (Fig. 2.4d). The most parsimonious models for all other soil function variables either had lower r^2 values, or were best modelled by null models.

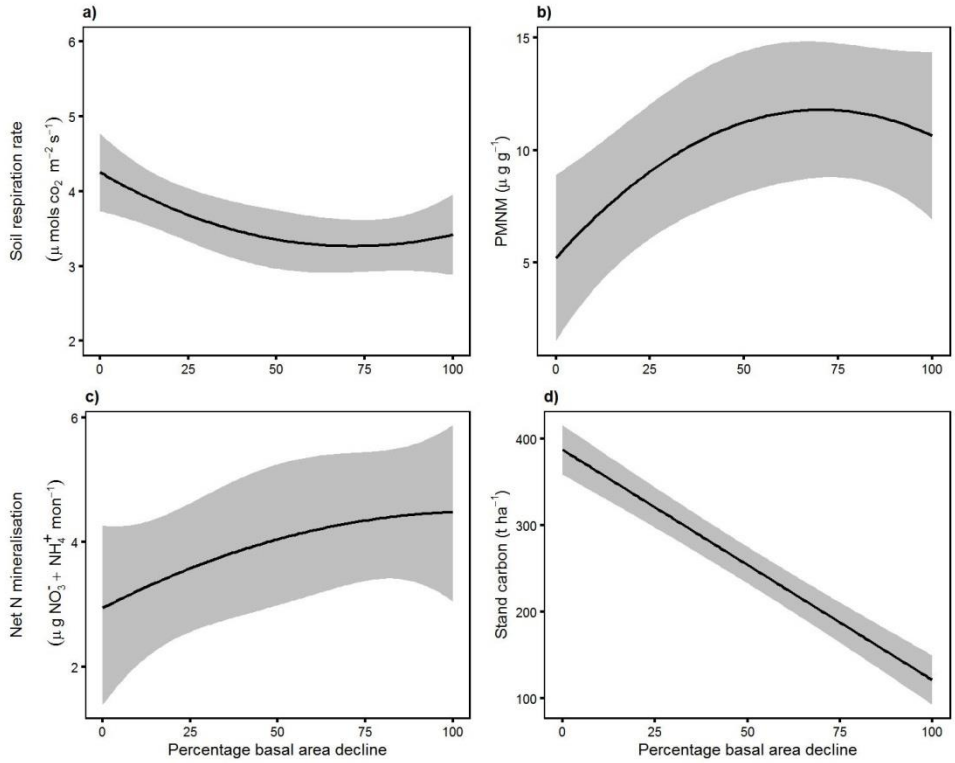

Fig. 2.4: Relationships between stage of dieback and ecosystem processes. Relationships between stage of dieback and a) soil respiration rate (n = 60); b) potentially mineralisable nitrogen in the mineral layer (PMNM) (n = 60); c) net mineralisation per month (n = 55); and d) total stand carbon (n = 60). The black lines represent prediction using the most parsimonious model coefficients and grey shading the 95% confidence intervals of the coefficients (marginal r^2 = 0.16, 0.07, 0.13, and 0.50 for a-d, respectively). Net mineralisation was measured as the amount of NH_4^+ and NO_3^- taken up by a resin capsule over a four-month period and then divided by 4 to obtain a value per month.

2.4.3. Ecological condition

A threshold response in the average sward height was defined by the most parsimonious model having linear and quadratic terms of BA loss (r^2 = 0.51; ΔAICc = 17.74) (Fig. 2.5a). Similarly, some of the seedling abundances (palatable seedlings, beech and oak separately and combined) showed thresholds effects, the most pronounced of which was the abundance of palatable seedlings, which had linear and quadratic terms of BA loss and a dung factor (r^2 = 0.29; ΔAICc = 55.51) (Fig. 2.5b). The understorey biomass also exhibited a threshold response as determined by the most parsimonious model, with linear and quadratic BA loss as its terms (r^2 = 0.38; ΔAICc = 5.81) (Fig. 2.5c). The condition of the remaining crowns was best described by a linear model, with only a linear BA loss term (r^2 = 0.16; ΔAICc = 2.22) (Fig. 2.5d).

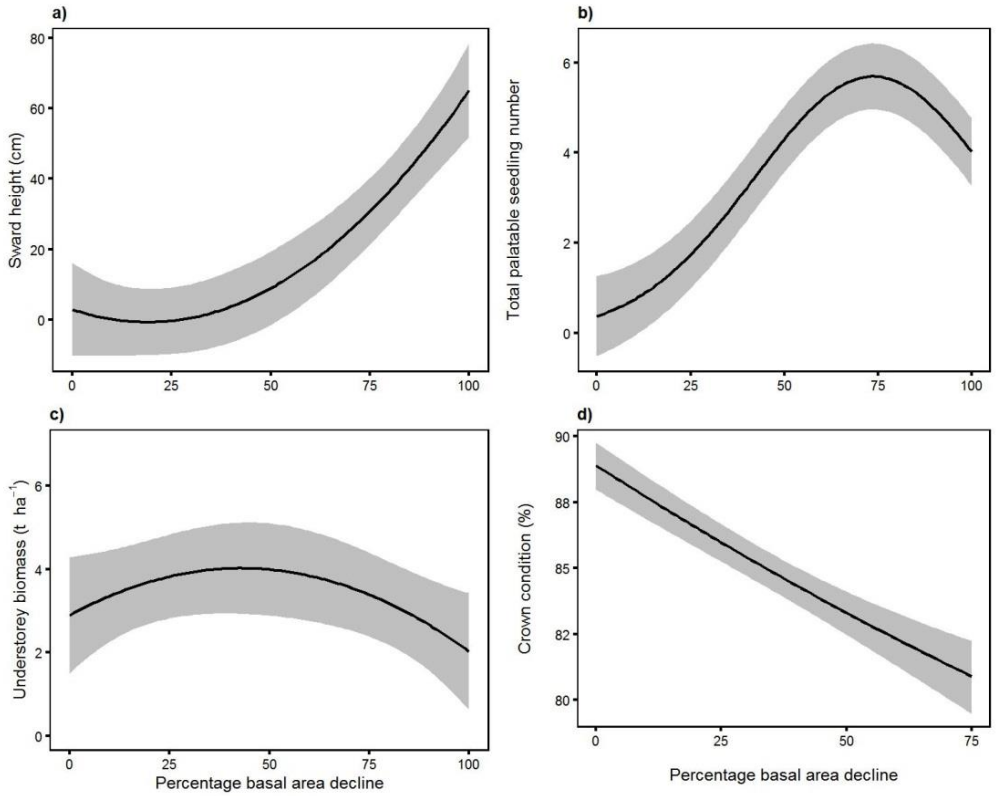

Fig. 2.5: Relationships between stage of dieback and ecosystem condition. Relationships between stage of dieback and (a) average sward height (n = 60); b) palatable seedling abundance per plot (n = 60); c) understorey biomass (n = 60) and d) the crown condition (n = 48). The black lines represent prediction using the most parsimonious model coefficients and grey shading the 95% confidence intervals of the coefficients (marginal r^2 = 0.51, 0.29, 0.38, and 0.16 for a-d, respectively).

2.5. Discussion

The results provide novel evidence of thresholds in biodiversity, ecosystem function and ecological condition in a forest ecosystem undergoing dieback. The most striking threshold responses were observed for biodiversity, specifically in the species richness of ECM fungi and epiphytic lichens, both of which started to decline sharply in the early stages of dieback, and ground flora, which increased until the latter stages of dieback. With respect to ecosystem function, a single threshold response was identified, namely in soil respiration rate. For ecological condition, thresholds were shown in sward height, which increased after initial dieback, and palatable seedling abundance, which initially increased across the gradient of stand dieback, but started to decline in the late stages.

As a result of deforestation and habitat fragmentation, research has reported a number of threshold responses in forest ecosystems, including in forest structure (De Filho and Metzger, 2006; Rocha-Santos et al. 2016), biodiversity loss (Fahrig, 2002; Ochoa-Quintero et al. 2015) and ecosystem service provision (Bodin et al. 2006). These studies all focused on the impacts of direct human-driven loss of forest cover (i.e. physical

removal) at the landscape scale. As far as is known, the current study is the first to report threshold responses over a gradient of stand dieback. Such dieback is increasing in response to environmental change in forests globally as a result of climate change, pest and disease attack, and increasing fire frequency (Bonan, 2008; Poulter et al. 2013; Lindner et al. 2014). Moreover, Allen et al. (2015) suggest that all forests may be vulnerable to climate-induced dieback in the future. If the responses observed in this study are widely applicable, the current results suggest that many forest ecosystems may potentially be characterised by threshold responses to environmental change.

The basis of ecological threshold theory is that rapid, non-linear changes are observed in ecosystem 'state' as a controlling variable changes (Scheffer et al. 2012). This implies that a relatively small increase in intensity or frequency of disturbance could cause rapid and abrupt declines in ecosystem condition, state or function, potentially creating highly degraded ecosystems (Muradian, 2001; Scheffer and Carpenter, 2003). This is concerning as thresholds may compromise the capacity of forest ecosystems to recover from future perturbations (Rompré et al. 2010; Lenton, and Williams, 2013), especially as anthropogenic pressures are predicted to intensify in future (Van Mantgem et al. 2009, Allen et al. 2010, 2015).

The precise mechanisms underlying ecological thresholds remain unclear (Scheffer et al. 2012). DeAngelis et al. (2012) and Scheffer et al. (2001) have highlighted that in order for a threshold to occur there must be a switch in an ecosystem from a self-regulating state (negative feedback) to one that is reinforced by further internal or external changes (positive feedback), i.e. a self-exacerbating state (Briske et al. 2006). The thresholds observed in this study may be the result of a number of positive feedback mechanisms including interactions between trees, soil microbes, soil chemistry and herbivory. For example, as trees die and degrade, symbiotic associations with ECM fungi are reduced (Teste and Simard, 2008; Corcobado et al. 2015). This can cause reductions in the abundance of other soil microorganisms owing to major modifications to water and nutrient exchanges (Ehrenfeld et al. 2005; De Vries et al. 2013; Crowther et al. 2014), which could create a positive feedback that substantially lowers plant survival and growth (Ehrenfeld et al. 2005; Simard et al. 2012). This could be evidenced by the decline in soil respiration rate that was observed in this study. In addition, the threshold observed in lichen species richness could be attributable to feedbacks between declining availability of bark substrate and changes in microclimate during the process of stand dieback (Sillett et al. 2000, Paltto et al. 2011).

In contrast to biodiversity measures, relatively little evidence was obtained here of threshold responses in measures of ecosystem function. In most cases, such measures varied non-linearly with BA loss, however they did not fulfil the $\Delta AICc \geq 3$ and marginal $r^2 > 0.15$ criteria. The exception was soil respiration rate. As soil respiration is the net result of the respiration of autotrophic (plant) and heterotrophic (microbial and mycorrhizal) activity (Hibbard et al. 2005), the initial declining trend may have been largely a result of decline in microbial activity in the soil owing to declining tree root density (Ryan and Law, 2005) and tree presence (Holden and Treseder, 2013).

A possible limitation in this study was the use of a space-for-time substitution in the experimental design, whereby the plots from a single site formed a chronosequence. This approach has known limitations, and even though the utmost was done to reduce any errors while using this method, the results should be interpreted with these limitations in mind. One of the major limitations relates to the interpretation of linearity. A chronosequence is assumed to be synonymous to a linear trend over time in whichever variable is being recorded. In this study, a unidirectional linear decrease in BA due to beech dieback was the variable. Thus, departures from linearity in response variables measured along the chronosequence provided evidence of a threshold. However, this uses the assumption that all the measured plots started at a comparable starting point. If the assumption was not accurate, departures from linearity could have arisen from and been influenced by historical variance amongst the field plots rather than just dieback. The assumption was based on the composition map of the New Forest from 1982 (Flowers and Tubbs, 1982) which showed that all the study sites had ≥ 90% canopy cover, with beech comprising 50%-90% of the canopy cover. This indicates that all the sites had a similar amount of beech canopy cover at the same time and could therefore by deemed to be a comparable starting point, although this is only based on one type of data. The other main limitations and steps taken to reduce them are discussed in section 6.3.3.

There were a few other issues relating to data interpretation which should be borne in mind when interpreting the results. First, in near-natural beech forests, the mortality of overstorey trees and regeneration are typically synchronized within a period of several decades, in patches extending over several hectares (Newton et al. 2013). The beechwoods of the New Forest differ from this situation, however, owing to the very high browsing pressure from large herbivores (Martin et al. 2015). As a result, beech regeneration is very sparse, and dieback of woodland stands often involves conversion to non-woodland habitat, principally grassland (Martin et al. 2015). In this study,

Second, mortality processes in trees are often highly complex and difficult to interpret (Franklin et al. 1987). This complexity is illustrated by other studies of stand dieback in tree species. For example, in studies of sudden dieback of aspen stands in North America, a number of different contributory and potentially interacting factors were identified, including drought, defoliation, extreme weather events and wildlife stem damage (Frey et al. 2004). Similarly, in their review of drought impacts on temperate forest stands, Bréda et al. (2006) identify a number of different physiological mechanisms that can increase the risk of tree mortality following drought, including decreased carbon and nutrient assimilation, breakdown of the photosynthetic machinery, and reduced storage of carbohydrates. Additional mortality factors could include significant storms that occurred in 1987 and 1990 and fungal pathogens attacks, which have been observed affecting beech the New Forest (Martin et al. 2015). Moreover, while factors such as insect attack, frost damage and bark stripping by herbivores were not analysed here, they could have had a significant impact on mortality patterns at this site. It should also be noted that the causes of the dieback observed could also potentially be correlated with the response variables; for example, increased incidence of drought could have concurrently affected both the survival of individual trees and the ECM fungi with which they are associated.

Further, it should be noted that data were evaluated from a single sample period along a gradient of live-tree BA. Ideally, data would have been obtained by sampling the same plots before and after the initiation of tree dieback. As noted above, the only long-term data available for this study relate to one of the 12 sites surveyed, namely Denny Wood (Martin et al. 2015). My interpretation of the results is therefore based on the assumption that the sequential dieback of beech that has been documented at that site also applies to the other sites in the New Forest where BA gradients were surveyed. In addition, it is important to note that I interpret here differences in the ecosystem composition, structure, and function among the plots as a response to dieback. It is conceivable that the variables measured could have differed across the study area prior to the onset of dieback. For instance, soil respiration might have varied across the study area prior to the onset of dieback, and this could have contributed to some of the variation in the magnitude of dieback observed. I have no way of testing whether all of the variables measured differed between measurement locations prior to the onset of dieback, and therefore our attribution of the responses observed to dieback is based on an assumption that there was no systematic variation in these variables prior to the occurrence of dieback.

Other issues that have a bearing on the interpretation of our results include our definitions of a threshold and dieback. Here we considered a response variable to show a threshold if it met the three criteria described in the Methods. As the criteria were developed by myself, different results may have been obtained had other criteria been adopted. Moreover, the definition of dieback we adopted was a decline in stand BA as the central measure. This is based on the results of a review of previous research conducted by Cantarello and Newton (2008), into the forest ecosystem characteristics that have most often found to be significantly related to maintenance of forest biodiversity. Of these, BA is one of the forest stand structure variables most consistently associated with forest biodiversity and with aspects of the functioning of forest ecosystems, such as carbon storage Cantarello and Newton (2008).

2.6. Conclusion and implications

Climate-induced forest stand dieback is rapidly increasing worldwide, in scale, magnitude, severity and speed (Allen et al. 2015). The occurrence of thresholds in forest ecosystems undergoing dieback is a major concern, since continued environmental change may produce non-linear declines in biodiversity and ecosystem function as the result of linear changes in disturbance. Results presented here indicate that such thresholds can occur over a forest dieback gradient. Importantly, the results show that species richness of ECM and epiphytic lichens start to decline sharply before there is a 50% decline in BA, which implies a shift from negative feedback mechanisms to strong positive feedbacks at this threshold. In contrast, only one ecosystem function measured, namely soil respiration rate, displayed a threshold response, suggesting that biodiversity and ecosystem function threshold responses are not necessarily closely coupled. Further research is required to identify the precise mechanisms underlying the threshold responses observed, and to examine whether the observed changes are reversible.

Chapter 3:

The effectiveness of condition assessments for detecting change across beech woodlands undergoing dieback

3.1. Abstract

Woodland condition assessments (CAs) are one of the most commonly used tools for determining woodland condition, the results of which are supposed to get fed back into adaptive management plans. In the UK, CAs are used in Sites of Special Scientific Interest (SSSIs). SSSI assessments are guided by Common Standards Monitoring (CSM) targets, which relate to different aspects of woodland condition. In this study, CSM targets were tested over a gradient of beech dieback, measured here as a decline in basal area of dominant tree species, to determine whether CSM CA scores were sensitive to dieback condition. This has never been tested before. Additionally, a wider range of non-CSM indicators were recorded to identify if other measures are sensitive to change in dieback. Specifically, the hypotheses tested were: i) Common Standards Monitoring condition assessment results will vary significantly over a gradient of environmentally-induced dieback; and ii) non-CSM indicators could be used to effectively determine different dieback stages. Results showed that overall condition scores derived from the CSM analysis varied slightly across the gradient of dieback. However, pairwise comparisons were only significant for one out of four CSM target lists tested. Moreover, overall condition scores did not vary consistently across the dieback gradient, contrary to what was expected. The results gave some support to the second hypothesis, as some non-CSM indicators could be used to differentiate between the stages of dieback. The findings presented here indicate that the use of CSMs in woodlands may currently have limited scope at determining dieback stages, and therefore one aspect of woodland condition, but that some individual indicators of condition could be used in future CAs. The issues raised by these results need to be addressed quickly to improve CAs in the future, especially in a period of rapid environmental change.

3.2. Introduction

Forests globally are facing an increasing number of threats from shifting forest disturbance regimes, novel stressors and changing environmental conditions. Consequently, the incidence of dieback and mortality of trees has increased in the last few decades (Breshears et al. 2009; Allen, 2009), a trend that may still be in its infancy (Allen, 2009; Allen et al. 2015). This form of severe ecosystem degradation results in the

simplification of forest structure, rapid changes in forest dynamics (Millar and Stephenson, 2015), major biodiversity and ES losses and declines in the health and condition of woodland ecosystems (MEA, 2005; Foley et al. 2007; Allen et al. 2015; Trumbore et al. 2015; Chapter 2 of this thesis), as well as making the already complex interactions of forests more unpredictable (Breshears et al. 2005; Woodall et al. 2009; Allen et al. 2010).

With so many aspects of forests threatened by novel disturbances and environmental changes, Protected Areas (PAs) – places with restrictions on damaging human activities – are essential for the conservation of biodiversity (IUCN, 1994). PAs are often also crucial for the protection and maintenance of flows of ES to people (e.g. Brockerhoff et al. 2013; Ferraro et al. 2014; Watson et al. 2014). Consequently, PAs are very important areas for conservation and the wider society as they offer the opportunity to directly manage an area for multiple benefits (Porter-Bolland et al. 2012). The main objectives of PAs relate to maintaining such benefits, thereby ensuring they do not change dramatically. However, the current effectiveness of PA management globally is often found to be low, with even basic objectives often not being met (Leverington et al. 2010; Porter-Bolland et al. 2012; Watson et al. 2014).

In the UK, Sites of Special Scientific Interest (SSSIs) are important PAs that have been set up to protect specific wildlife, habitats or other rare geological features. SSSIs are afforded legal protection through the UK government, who have a responsibility to make sure that individual SSSIs are adequately conserved and protected (Natural England, 2013). SSSIs set such a high standard for protection of habitats that it has been recommended that other semi-natural habitats are managed and assessed in a similar way (Defra, 2011).

To ensure that SSSIs and other PAs are maintained and meet objectives, they must be monitored regularly and assessed effectively (JNCC, 2003; JNCC, 2004; Leverington et al. 2010; Porter-Bolland et al. 2012). In SSSIs, each habitat of concern (known as a unit) is assigned to a relevant category for further action (JNCC, 2004; Gaston, 2006) based on monitoring-derived condition assessments (CAs). The categories each unit can be assigned to are on a discrete category spectrum, going from Favourable to Unfavourable condition (JNCC, 2003). The condition result is fed back to the assessment team, detailing if and what needs to be done or changed to produce Favourable site status (Fig. 3.1; JNCC, 2003; Gaston et al. 2006).

CAs in SSSIs are carried out through Common Standards Monitoring (CSM) guides that have been developed by JNCC (1998), and which initially were intended to

act as a rapid and robust method for assessing the general condition of conservation sites (Williams, 2006). CSMs detail specific attributes and suggested targets for different habitats. For woodland, the mandatory attributes that need to be included in assessment are: i) extent; ii) structure and natural processes; iii) regeneration potential; iv) tree and shrub composition; and v) indicators of local distinctiveness (JNCC, 2003; see JNCC (2004) for further explanation of each). Furthermore, CSM targets, which are required to pertain to the attributes, should: 1) be site-specific; 2) be relevant and practical; 3) describe state, not management; 4) be ranges rather than single figures; and 5) be triggers for action (JNCC, 2004). Following these CSM guidelines, target lists are created by the managers of each SSSI. Target lists consider generic targets, but also take into account geographic variation and local features (Williams, 2006). If all targets are met then the unit is considered to be Favourable (JNCC, 2003). Favourable for woodlands is a balance between canopy cover, dead wood, regeneration potential and composition (JNCC, 2004).

Despite its acknowledged limitations, which, like all CAs, include trade-offs between resource availability and the amount and quality of data collected (Hockings, 2003; JNCC, 2004; Niemi and McDonald, 2004; Carlsson et al. 2005; Fennessey et al. 2007), CSM CAs provide simple ways of monitoring SSSIs for habitats, species and geological features in one assessment – a task that has historically been difficult to achieve (Williams, 2006; Fennessey et al. 2007). However, it has been questioned whether such measures are too generalised to be useful for conservation (Niemi and McDonald, 2004; Fennessey et al. 2007; Oliver et al. 2014). For example, Davies et al. (2007) found that the targets specified in grassland CSM CAs were too generalised, due in part to targets being too focused on vegetation metrics rather than the conditions needed for specific wildlife (e.g. butterflies). If such measures are too general, CAs could be insufficient to effectively determine changes occurring within PAs (Failing and Gregory, 2003; Jackson and Gaston, 2008), consequences of which could include biodiversity, ES and ecosystem functions losses or changes going unnoticed until such a time that it is too late for management to improve conditions (Hockings, 2003; Failing and Gregory, 2003; EEA, 2016). Accordingly, Davies et al. (2007) and Fennessey et al. (2007) suggest using a wider range of monitoring targets to meet these needs. In woodlands, additional targets could relate to ecological indicators of composition, structure and function, the three main attributes that describe forest condition (Noss, 1999; Gao et al. 2015; Lawley et al. 2016).

To enable the most appropriate management actions to maintain or improve condition of PAs, CAs need to be effective at detecting changing ecosystem condition, hence the importance of CAs in ecosystems (Gaston et al. 2006; Trumbore et al. 2015).

However, the effectiveness of CAs has rarely been tested (Gaston et al. 2006; Watson et al. 2014), meaning that it is unknown whether CA results are sensitive to variation in condition (Gaston et al. 2006). This extends to CSM approaches, which have never explicitly been tested, as far as is known. To test whether current CSM targets can effectively determine differences in one aspect of woodland condition, namely beech dieback, the targets were measured across a gradient of dieback of dominant tree species. Additionally, other ecological indicators were assessed across the dieback gradient to determine whether they could be used in future CAs by being able to detect changing condition. The specific hypotheses tested were: i) Common Standards Monitoring condition assessment results will vary significantly over a gradient of environmentally-induced dieback; and ii) non-CSM indicators could be used to effectively determine different beech dieback stages.

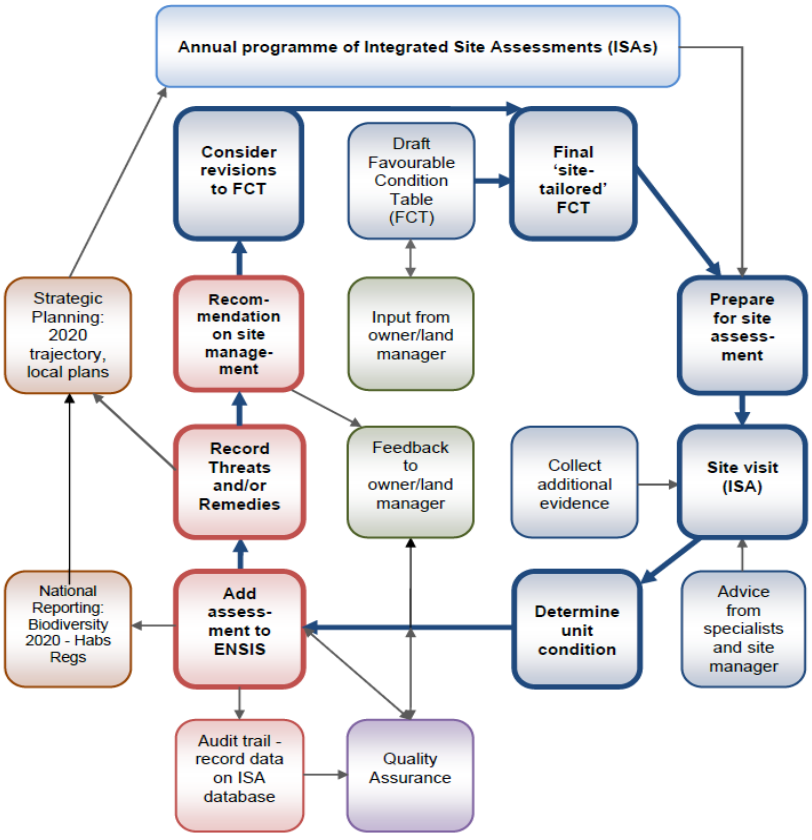

Fig. 3.1: A schematic diagram of the monitoring and condition assessment process for SSSIs. Reproduced from Natural England (2013).

3.3. Materials and methods

3.3.1. Study area

The Ancient and Ornamental (A&O) woodlands of the New Forest, named in the New Forest Act 1877, provide the greatest area of semi-natural vegetation in lowland Britain (Tubbs, 2001) and are the focus of this study (Fig. A3.1). Although there is no formal definition of what A&O woodlands actually mean, they are generally thought of as woodland that originated before the 18th century (Wright and Westerhoff, 2001). The A&O woodlands generally consist of canopies of beech (*Fagus sylvatica*) and pedunculate oak (*Quercus robur*) interspersed with birch (*Betula pendula*), yew (*Taxus baccata*) and holly (*Ilex aquifolium*) and support a wide array of diverse wildlife. The A&O woodlands are also considered pasture woodland, which is a habitat that supports grazing livestock and trees. Due to the history of the A&O woodlands, they are characterised by a range of trees of different ages, both living and dead, which provide habitat for many rare lichen, fungi and moss species (Tubbs, 2001; Newton, 2010; Sanderson, 2010; Stern, 2010) and characteristic open spaces (Wright and Westerhoff, 2001). Scots pine stands are present in 153 ha of the A&O (Wright and Westerhoff, 2001), but they were excluded as units in this study. For a full description of the New Forest, see the section 1.6 of this thesis.

3.3.2. Experimental design

A gradient of beech dieback was conceived using the stand basal area (BA) of living beech trees (see Chapter 2 of this thesis), as calculated by Cantarello and Newton (2008). From the average BA of 12 'Intact' (i.e. closed canopy) beech stands, the BA of the other four stages (Slight, Moderate, Major and Total dieback) were calculated as a percentage less (Slight dieback = 75% BA of the Intact average, Moderate = 50% BA of Intact, etc.). Other criteria included in dieback stage selection were the requirement of presence of standing or lying dead wood, and increasing canopy openness. Twelve sites were used overall, meaning each stage had 12 replicates, totalling 60 plots all together. The plots for each stage were 20 m^2 (0.04 ha), and the sites covered a variety of areas within the A&O woodlands, specifically the beechwoods. To test whether CSM condition assessment results and other non-CSM indictors varied significantly over the beech dieback gradient, CSM targets and other potential indicators were recorded across each of the 60 plots.

3.3.3. CSM target lists

Four different sets of CSM target lists were tested overall to see how effective each one was at detecting changes over the dieback gradient. These were: two CSMs checklists specifically created for the New Forest, one for pasture woodlands (Appendix 3.2) and one for Ancient and Ornamental (A&O) woodlands (Appendix 3.3); an example list with attributes and targets for New Forest pasture woodlands from the appendix of a Wiltshire habitat strategy report (Appendix 3.4; herein known as WiltPast); and one, the Generic List, created from the general CSM woodland targets, as suggested in JNCC (2004). There are slight differences in the targets used in the Generic List compared to the individual New Forest lists, as the former focuses on generic targets and the latter includes targets specific to the New Forest. Both the pasture woodlands and A&O checklists were used as the study area is technically classed as both of these habitats. For all CSM lists, manual felling of trees, drainage maintenance and other safety work was included as a single target, following the example on the original pasture CSM sheet (Appendix 3.2). See Appendix CD, CD3.1, for the targets used in each CSM list and explanations of why targets were included or excluded from the Generic List.

3.3.4. Non-CSM indicators

Non-CSM indicators were defined as commonly-used forest condition indicators that were not specifically featured as targets in the CSM target lists, or those that were but were not empirically measured in CSM targets. Dead wood is an example of the latter; in CSM it was put into a category, while for the non-CSM indicator the actual volume of dead wood was recorded.

Consideration was given to the amount of effort needed to collect each indicator, as well as how much time it would take to record. Thus, indicators were divided into three categories, depending on how resource intensive assessing the indicator was, since CSM methodology states that assessments should take place within a limited time and do not rely on specialist knowledge (JNCC, 2004). These categories were: 1) single-time, easy to assess indicators, which were measurements that could be recorded in the field in a single visit with no prior ecological knowledge required; 2) single-time assessment, ecological skill indicators, which were the same as previous, but required a specific ecological skill (e.g. identification of different species); and 3) harder to record indicators, which were measurements that required extraction of material (e.g. soil), laboratory analysis and/ or repetition of analyses.

Non-CSM indicators included metrics of biodiversity, function and structure. Biological indicators collected included ground flora, epiphytic lichen and ectomycorrhizal fungi (ECM), which were all recorded in all plots by experts on that taxon. Surveying of all plots was carried out in summer (July/August) for ground flora, winter (late October/ early November) for ECM and spring (March) for lichen. Ground-dwelling arthropods were measured in five sites using eight pitfall traps placed regularly around the centre of each plot. Pitfall trap contents were collected eight times from late May to late July. DNA barcoding was then used to identify arthropod species (see Appendix 2.2). Sward height was recorded in the summer as a mean of five measurements in the plot, one in the centre and four halfway between the centre and respective corners of the plot (the four halfway points created a nested sub-plot).

Structural stand indicators, including sapling and seedling measures, were all recorded in the summer. The length, breadth and circumference of dead wood were measured using appropriate tape measures. Where the height of standing dead wood could not be measured by hand, height was calculated based on clinometer measurements (as was the height of living trees). Dead wood volume was subsequently calculated from cumulative cylindrical equations results. Ground cover of bracken, litter, grass, moss, bare ground, bramble (*Rubus* spp) and holly shrub (< 1.3 m) was recorded as a percentage of the plot. Canopy and understorey openness was measured using a densiometer at the sub-plot corners, and then averaged. Understorey cover was defined as crown of trees less than 8 m in height which did not have canopy trees above them. Structural crown loss, leaf loss, discolouration and understorey condition were measured as a percentage of the potential of the tree, based on the average of two recorders, from as many angles as possible. Biomass was calculated based on diameter at breast height (DBH) and average height measurements, and then calculated per hectare. From the range of full of DBH amounts, beech trees were divided into very small, small, medium, large and extra-large classes, based on quantile amounts.

Ecosystem functions measured included soil respiration rate; net mineralisation, net ammonification and net nitrification; and nutrient concentrations and cation exchange capacity (CEC) of the soil. Browsing indicators included dung count metrics based on total counts and relative condition, percentage of bramble and holly shrub eaten, percentage browseline of palatable (e.g. beech and oak) and unpalatable (e.g. holly), debarking and trampling amount. For more detailed methods, see Appendix 2.1.

3.3.5. Data analysis

Initially the individual CSM targets were given a 1 when met, and 0 when not met. These results were then combined into the four individual CSM target lists, so that each could reach a possible total score of the number of targets assessed in that particular list. The percentage of targets met were then calculated for each target list to standardise assessment. To test whether the overall CSM condition results for each target list varied significantly across the dieback condition gradient, one-way ANOVA and subsequent Tukey's post-hoc tests were used with the diebacks stage as the discrete independent variable. For the CSM target lists, ANOVAs were analysed with site as a random effect to correct for any natural variation between the different sites studied, as well as without site as a random effect, as this could be important in comparing assessments nationally. Non-CSM indicators were individually assessed using one-way ANOVAs with site as a random effect and subsequent Tukey's post-hoc tests in a similar way to the CSM target lists, but with empirical values of the indicators. CSM target lists and non-CSM indicators were determined to be a useful indicator of condition if a one-way ANOVA and subsequent Tukey's post-hoc gave significant results between at least two dieback stages. All analyses were performed in R 3.1.2. (R Development Core Team, 2011, http://www.R-project.org).

3.4. Results

3.4.1. CSM target lists

Overall, significant differences were recorded across the gradient of dieback stages for the four CSM target lists, based on ANOVA results, when site was corrected for: NF A&O (X^2 (4) = 10.45, p = 0.03) (Fig. 3.2A; Table 3.1); NF pasture woods (X^2 (4) = 11.36, p = 0.02) (Fig. 3.2B; Table 3.1); WiltPast (X^2 (4) = 11.73, p = 0.02) (Fig. 3.2C; Table 3.1); and the Generic List (X^2 (4) = 10.49, p = 0.03) (Fig. 3.2D; Table 3.1). However, Tukey's Bonferroni-corrected post-hoc tests revealed no significant differences between any of the dieback stages for any of the CSM target lists condition scores (Table 3.2). It should be noted though that some authors argue against using Bonferroni corrections for biological applications (e.g. Moran, 2003; Nakagawa, 2004). Without Bonferroni-corrected p-values, only a single significant difference was exhibited between the stages, and then only for one of the CSM target lists. This was between the Intact and Major stage for NF pasture woods (Table 3.2), where there was a significant increase in terms of the percentage of targets met from the Intact to Major stage.

There was not much variability for some CSM targets over the different stages of dieback (Fig. 3.3; Appendix 3.6). Vegetation over 10 cm (v10) was the only measurement that increased at every subsequent stage of dieback, based on the percentage that that target was met over the 12 replicates of each stage. Starting from the Slight dieback stage, the signs of tree stress on trees > 80 DBH decreased over the gradient. All other CSM measures did not vary systematically over the gradient.

3.4.2. Non-CSM indicators

Sixty-eight variables were measured over the dieback gradient, which can be split into three broad categories: i) single-time, easy to assess criteria – no prior knowledge required; ii) single-time assessment requiring ecological skills; and iii) harder to record indicators, such as the content of the soil. Overall, 38 variables showed significant differences across the dieback gradient. However, only 26 showed significant differences between some or all of the dieback stages individually, based on the post-hoc test results.

3.4.2.1. Single-time, easy to assess indicators

Beech biomass, which decreased as dieback increased, was unsurprisingly highly significant (X^2 (4) = 470.24, p <0.01) (Fig. 3.4a), with significant post-hoc comparisons across all the dieback stages, at a 0.05 level. Similarly, the abundance of beech trees which declined over the dieback gradient showed a high level of significance (X^2 (4) = 180.57, p <0.01) (Fig. 3.4b), with only post-hoc comparisons of Intact-Slight, Moderate-Major, and Major-Total showing non-significance.

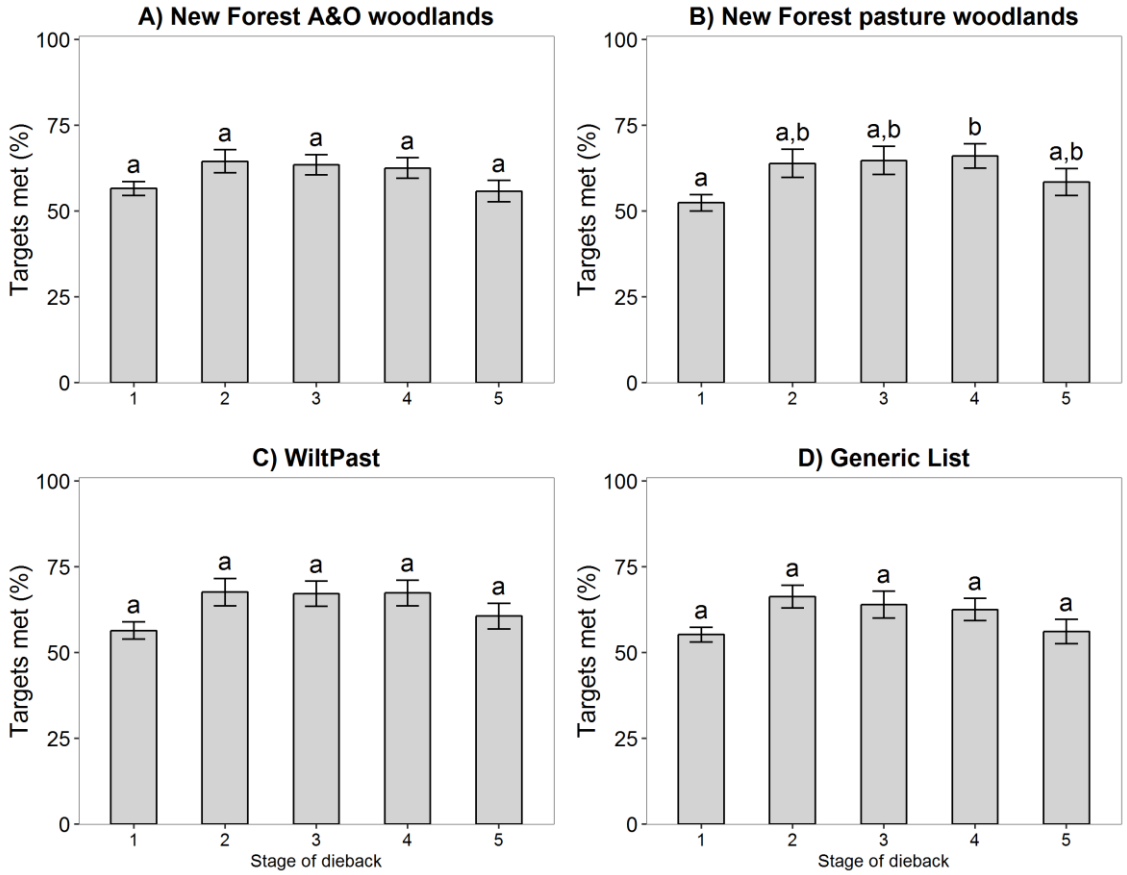

Fig. 3.2: Mean values of the percentage of targets that were met at each stage of dieback (1-5; Intact to Total dieback) for the CSM target lists: A) New Forest A&O woodlands; B) New Forest pasture woodlands; C) WiltPast; and D) the Generic List. For specifics of the individual CSM target lists, see text (section 3.3.3) and CD, CD3.1. The black bars indicate the standard error of the mean. Means grouped by the same letter are not significantly different ($p < 0.05$, Tukey HSD test). Bonferroni-corrected *p*-values are not displayed on these graphs, but can be found in bold in Table 3.2.

Table 3.1: Mean values of the percentage of targets that were met at each stage of dieback for the individual CSM target lists. SE represents the standard error of the mean.

Dieback stage	**Mean**	**SE**	**CSM target list**
1 – Intact	52.38	2.38	New Forest pasture woodlands
2 – Slight	63.87	4.13	New Forest pasture woodlands
3 - Moderate	64.74	4.13	New Forest pasture woodlands
4 – Major	66.07	3.53	New Forest pasture woodlands
5 – Total	58.47	3.91	New Forest pasture woodlands
1 – Intact	56.55	2.05	New Forest A&O woodlands
2 – Slight	64.47	3.36	New Forest A&O woodlands
3 - Moderate	63.51	2.94	New Forest A&O woodlands
4 – Major	62.50	3.02	New Forest A&O woodlands
5 – Total	55.76	3.11	New Forest A&O woodlands
1 – Intact	56.41	2.56	WiltPast
2 – Slight	67.57	4.01	WiltPast
3 - Moderate	67.15	3.65	WiltPast

4 – Major	67.36	3.74	WiltPast
5 – Total	60.58	3.79	WiltPast
1 – Intact	55.21	2.15	Generic List
2 – Slight	66.32	3.29	Generic List
3 - Moderate	63.96	3.89	Generic List
4 – Major	62.50	3.23	Generic List
5 – Total	56.11	3.51	Generic List

Canopy openness (X^2 (4) = 484.71, p <0.01) (Fig. 3.4c) was also significant different over the dieback gradient, increasing with the stage of dieback. Only the Intact-Slight comparison showed non-significance. The amount of carbon stored in the stand significant decreased with dieback (X^2 (4) = 198.39, p <0.01) (Fig. 3.4d), with the only non-significant comparisons between the Slight-Moderate and Major-Total comparisons. Other single-time, easy to assess criteria that showed significant ANOVA and post-hoc test results were the average sward height (X^2 (4) = 70.27, p < 0.01), with all the post-hoc tests containing the Total stage showing significant increases from the first two stages, based on post-hoc tests at 0.05 level; bracken cover (X^2 (4) = 31.89, p < 0.01), the Total stage of which was significantly higher than the first three stages; and the total quantity of lying dead wood (X^2 (4) = 40.15, p < 0.01), which had three significant stage-based comparisons, with Total being significantly greater than deadwood at the Intact or Slight dieback stages. The proportion of holly browsed exhibited a significant overall effect (X^2 (4) = 9.80, p = 0.04), but no significant post-hoc results.

3.4.2.2. Single-time assessment, ecological skill indicators

All of the species richness measures differed significantly over the dieback gradient. Ground flora species richness was one particularly sensitive measure (X^2 (4) = 71.26, p < 0.01) (Fig. 3.5a), with the Intact stage being significantly lower than all the later stages subsequent to the Slight dieback stage, and the Slight stage being significant lower than the Major and Total stages. Lichen species richness on beech differed significantly between the Total stage and all other stages, exhibiting lower richness at the Total stage (X^2 (4) = 57.69, p < 0.01) (Fig. 3.5b), based on Bonferroni-corrected post-hoc tests. ECM richness was sensitive across the dieback gradient (X^2 (4) = 68.27, p < 0.01) (Fig. 3.5c), with general decreases in richness as dieback increased. Specifically, mean ECM of the Moderate stage was significantly lower than the Intact stage, and the Total stage mean ECM was significantly lower than the Moderate stage by 40%, 9.75 compared to 3.83 species per plot. The dieback stage significantly influenced ground-dwelling arthropod richness (X^2 (4) = 15.13, p = 0.03). However, only the Intact and Total differed

significantly based on Bonferroni-corrected post-hoc tests, where Total had a significantly higher mean ground-dwelling arthropod richness.

3.4.2.3. Harder to record indicators

Of the harder to record indicators measured in this study, the cation exchange capacity (CEC) of sodium and calcium, and the ratio of both of these, all differed significantly over the dieback gradient. Sodium CEC (X^2 (4) = 36.95, $p < 0.01$) (Fig. 3.5d) exhibited significant declines between Intact-Major, Intact-Total, Slight-Major and Slight-Total stages, at a 0.005 level. Calcium CEC (X^2 (4) = 11.39, $p = 0.02$) only showed a significant increase between the first (Intact) and last (Total) stage however. The Na-Ca ratio (X^2 (4) = 30.684, $p < 0.01$) showed significant declines in post-hoc comparisons between the Intact-Major and Intact-Total stages. The respiration rate of soil was another one of the harder to collect variables that showed overall significant change over the dieback gradient (X^2 (4) = 12.96, $p = 0.01$), however post-hoc tests showed no significant differences between the different stages. The same was true for net N mineralisation (X^2 (4) = 12.56, $p = 0.01$). For all the non-CSM indicators that differed significantly across the gradient, see Appendix 3.7. For all non-CSM ANOVA and post-hoc results, see CD, CD3.2.

3.5. Discussion

3.5.1. CSM indicators

Protected areas that incorporate forests are needed to help maintain biodiversity, ES and ecosystem processes in a world that is increasingly facing more environmental threats (Porter-Bolland et al. 2012; Watson et al. 2014). The degree to which PAs can carry out these functions are dependent on the condition of the PA. To that end, the aim of the present study was to document how well CSM condition assessments, which are required to be undertaken in SSSIs by law, could detect change over a gradient of condition (forest stand dieback, in this case). This is a focus which has previously received very little attention (Jackson and Gaston, 2008). CSM condition assessments specifically have never been tested in this way, as far as is known. The main results were that overall condition for each stage for every CSM target list was > 50% and that condition from each CSM target list significantly varied across the gradient of dieback, based on the results of ANOVAs. However, pairwise comparisons between all stages, which are generally used to lessen the chance of Type I statistical decision errors, determined that there was only significant difference between two individual stages for a single target list despite the

variation in condition for structure and composition (see Chapter 2's results). This was for the NF pasture woodlands CSM list between the Intact and Major dieback stages. Therefore, based on pairwise tests, this indicates that for three out of four CSM target lists analysed, CSM woodland condition did not systematically vary over the dieback gradient and was therefore not sensitive to condition change in the context of beech BA dieback. This indicates that condition categories may not be ecologically useful, echoing the concerns of others (Gaston et al. 2006).

One of the most interesting findings here was that none of the overall condition scores derived from the CSM target lists analysed changed in a systematic way across the dieback gradient, either positively or negatively; the highest mean condition was the Major dieback stage for the New Forest pasture woodlands target list and the Slight dieback stage for the other three, while Intact was the most similar to Total dieback (Table 3.1). Oliver et al. (2014) showed a similar phenomenon when looking at two sites, one with full functionality and one with zero functionality – both had the same overall condition score. They showed that other targets tested - those pertaining to structure and composition - compensated for the lack of functionality in the latter site. Based on the trends of individual CSM targets that were met (Fig. 3.3; Appendix 3.6; CD, CD3.1) at each dieback stage in this study, changes between the stages were either barely detected at all (e.g. having at least one sapling of oak or beech (Nat.Sap)) or they had opposite and therefore compensatory effects. For example, the frequency of the < 1% non-native species in plot (NNS) target being met generally decreased with dieback, which was compensated in part by the dead wood (DW_tot) target being increasingly met with dieback. While this makes ecological sense as disturbed sites are more prone to invasive species colonisation (or invasive species may drive the disturbance) (MacDougall and Turkington, 2005) and dying trees create more dead wood (Koop and Hilgen, 1987; Rugani et al. 2013), the difference in these attributes was not identified through the use of a single final condition score (Fennessey et al. 2007; Oliver et al. 2014).

A target common to all CSM targets lists tested here was that beech and oak should comprise 10% of all saplings (OBsap). However, this target was rarely met, the reason being due to the local abundance of holly (*Ilex aquifolium*), a shade-tolerant temperate species (Peterken and Lloyd, 1967; Sack, 2004), which comprised the majority of saplings observed in this study. Holly is widespread in the understorey of beechwoods in New Forest (Tubbs, 2001; Martin et al. 2015) occurring more than in a lot of other beech-dominated woods (Peterken and Lloyd, 1967). Additionally, due to the high herbivory pressure of the New Forest, regeneration of beech is often prevented (Putman

et al. 1989). This lack of local specificity of some targets meant the amount of times they were met over the dieback gradient did not vary much, despite one of the advantages of CSMs purporting to be that it can deal with geographical variation and local distinctiveness (JNCC, 2003; Williams, 2006). Analogous conclusions are obtained when comparing the generic (i.e. Generic List) and more specific A&O woodland and the WiltPast lists – none of the specific CSM lists condition scores were significantly different to the generic list at any stage of dieback (Appendix 3.8). For this reason, CSMs could benefit more from a wider, more site-specific range of indicators in the latter cases (Gaston et al. 2006; Davies et al. 2007; Jackson and Gaston, 2008).

Although the CSM CA results demonstrated little sensitivity to variation in condition over the beech dieback gradient, other factors should also be considered when interpreting the results presented in this study, largely pertaining to its limitations. First, CSM guidance advises a structured walk to assess condition (JNCC, 2004). To meet the plot selection criteria of the methods of this study, which was necessary for statistical rigour, single areas were used, and not the entirety of the habitat area. If the whole area was observed, plots identified as Total dieback may have been in the minority, which could mean the rest of the area is in relatively good condition. Second, there was no information available about the relative weighting that assessors give each target. For instance, lack of beech and oak saplings may have been given higher priority than ground disturbance being < 1% for the regeneration potential attribute, which may have changed the overall results, as explored by Oliver et al. (2014). Third, the CSM guide also asks how much woodland could be lost without the values of the habitat reducing (JNCC, 2004), something which was not considered here. Obviously, however, the last two points would mean that results would be subject to higher levels of subjectivity, an already known issue for CSMs (Gaston et al. 2006; Jackson and Gaston, 2008). Lastly, no extent targets were considered in this study owing to plot restrictions, but extent is one of the mandatory attributes that is required to be measured (JNCC, 2004).

Table 3.2: ANOVA and post-hoc test results of the CSM target lists across the stages of woodland dieback. The 'Site as a random effect' column indicates whether site was included as a random effect in the analysis. *F*-values are for the ANOVAs where site was not corrected for, and the X^2 values are for the ANOVAs where site was corrected for. The 'Pairwise test' column indicates which controlling procedure was used for the pairwise comparisons. The 'Pairwise comparison stages' indicates which two stages of woodland dieback were compared using the pairwise test: Intact (Int), Slight (Sli), Moderate (Mod), Major (Maj) and Total (Tot), and shows the p-values for the pairwise comparisons tests below. Bold values indicate significant results.

CSM target list	Site as a random effect?	df	Anova result		Pairwsie test	Pairwise comparison stages									
			F/ X^2	*p-value*		Int-Sli	Int-Mod	Int-Maj	Int-Tot	Sli-Mod	Sli-Maj	Sli-Tot	Mod-Maj	Mod-Tot	Maj-Tot
A and O	Yes	4	10.451	**0.033**	Tukey	0.174	0.293	0.456	0.999	0.999	0.982	0.106	0.999	0.193	0.326
		4			Bonferroni	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	No	4	1.945	0.116	Tukey	0.324	0.455	0.607	1.000	0.999	0.989	0.235	0.999	0.346	0.488
		4			Bonferroni	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Generic List	Yes	4	11.726	**0.020**	Tukey	0.049	0.197	0.376	0.999	0.978	0.881	0.087	0.996	0.299	0.514
		4			Bonferroni	0.486	1.000	1.000	1.000	1.000	1.000	0.873	1.000	1.000	1.000
	No	4	2.263	0.074	Tukey	0.129	0.333	0.518	1.000	0.986	0.921	0.191	0.998	0.443	0.641
		4			Bonferroni	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Pasture	Yes	4	11.362	**0.023**	Tukey	0.111	0.071	**0.033**	0.704	1.000	0.991	0.788	0.999	0.680	0.499
		4			Bonferroni	1.000	0.708	0.327	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	No	4	2.379	0.063	Tukey	0.191	0.137	0.078	0.768	1.000	0.993	0.836	0.999	0.748	0.591
		4			Bonferroni	1.000	1.000	0.783	1.000	1.000	1.000	1.000	1.000	1.000	1.000
WiltPast	Yes	4	10.492	**0.033**	Tukey	0.086	0.109	0.097	0.881	1.000	1.000	0.512	1.000	0.575	0.543
		4			Bonferroni	0.865	1.000	0.974	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	No	4	2.006	0.106	Tukey	0.194	0.227	0.210	0.922	1.000	1.000	0.643	1.000	0.695	0.669
		4			Bonferroni	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

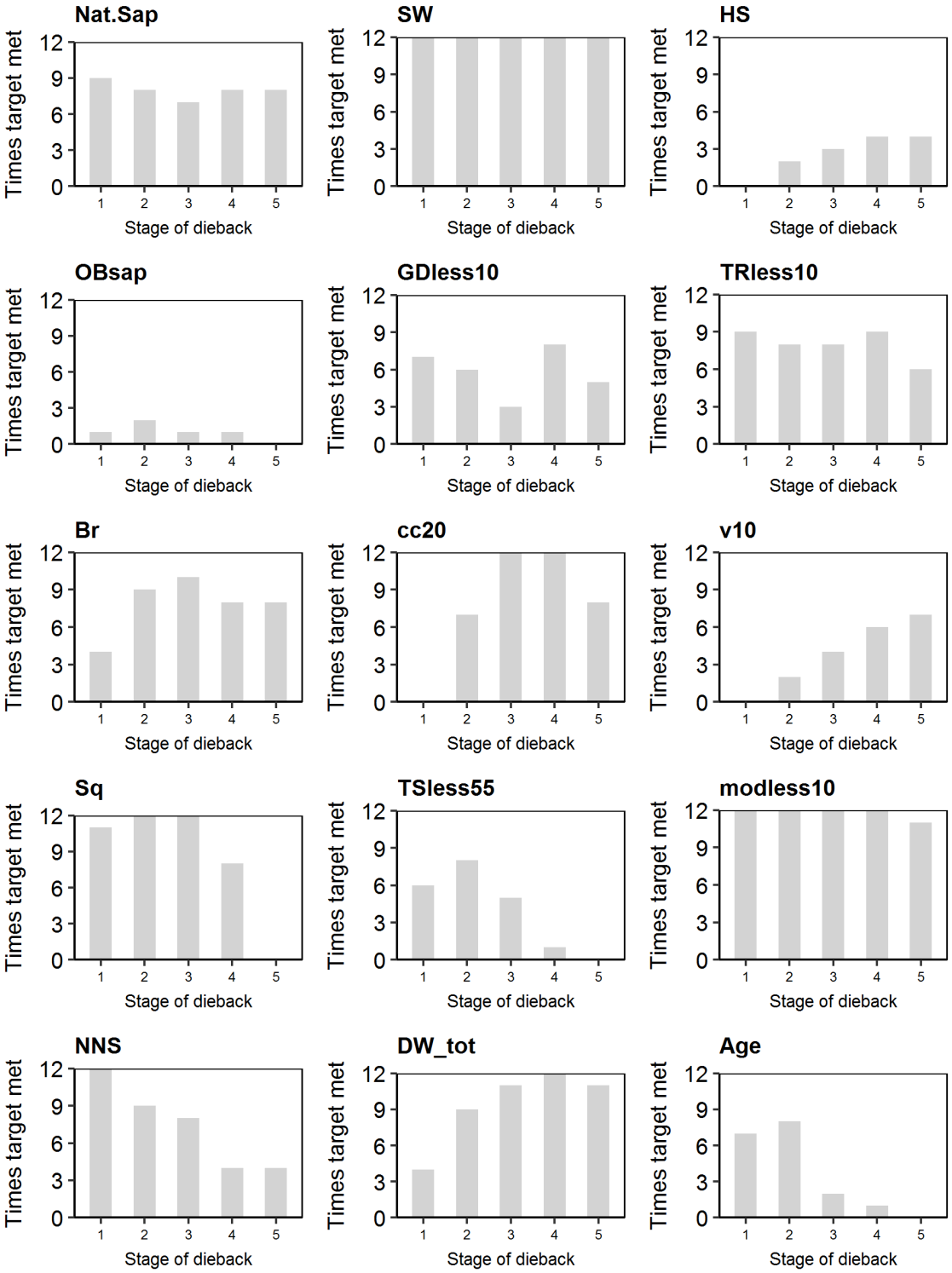

Fig. 3.3: A selection of CSM targets showing the variation in the number of times that target was met across the different stages of dieback. Each target is represented on a separate graph, with the title indicating the target. See Appendix 3.6 for explanation of title abbreviations.

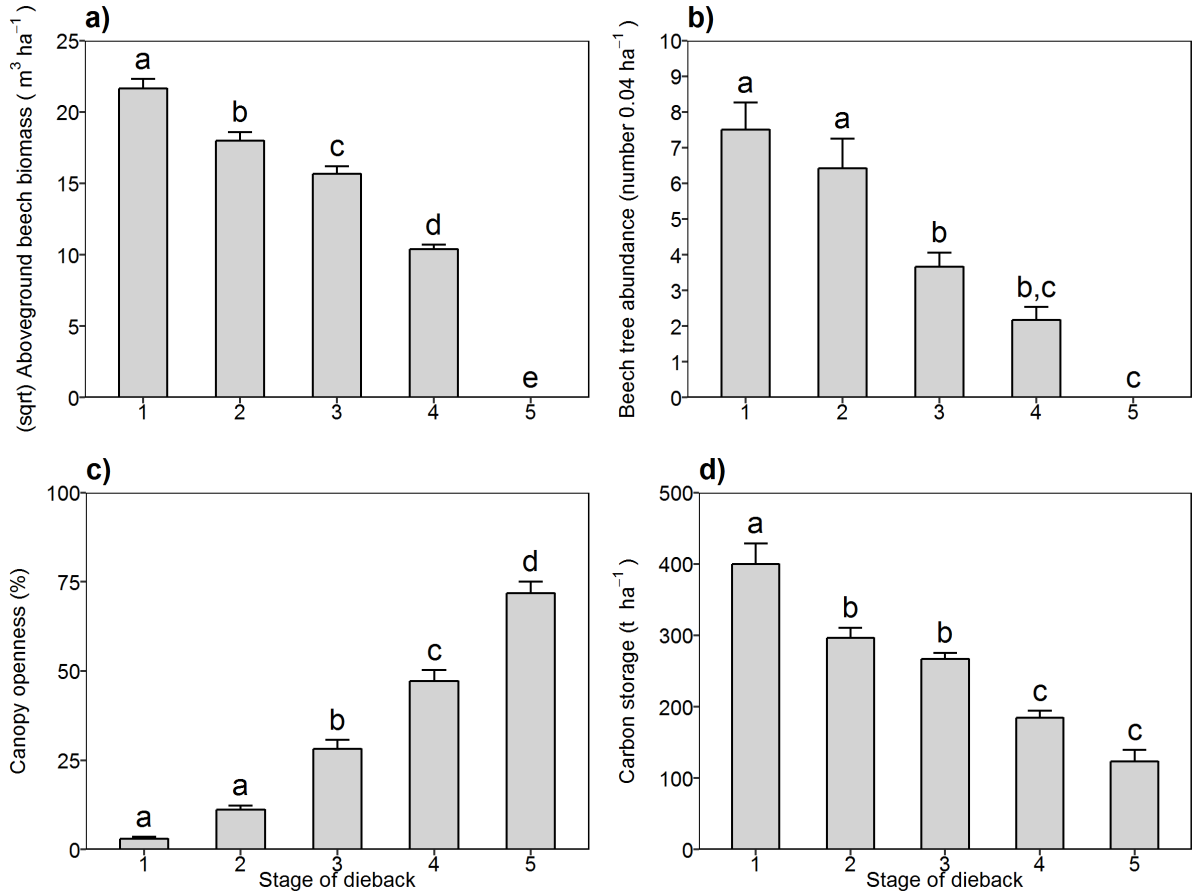

Fig. 3.4: Mean values of single-time, easy to assess indicators measured across the stages of dieback. The black bars indicate the standard error of the mean. a, b, c, and d are aboveground beech biomass, beech tree abundance, canopy openness and carbon storage, respectively. Means grouped by the same letter are not significantly different ($p < 0.05$, Tukey HSD test).

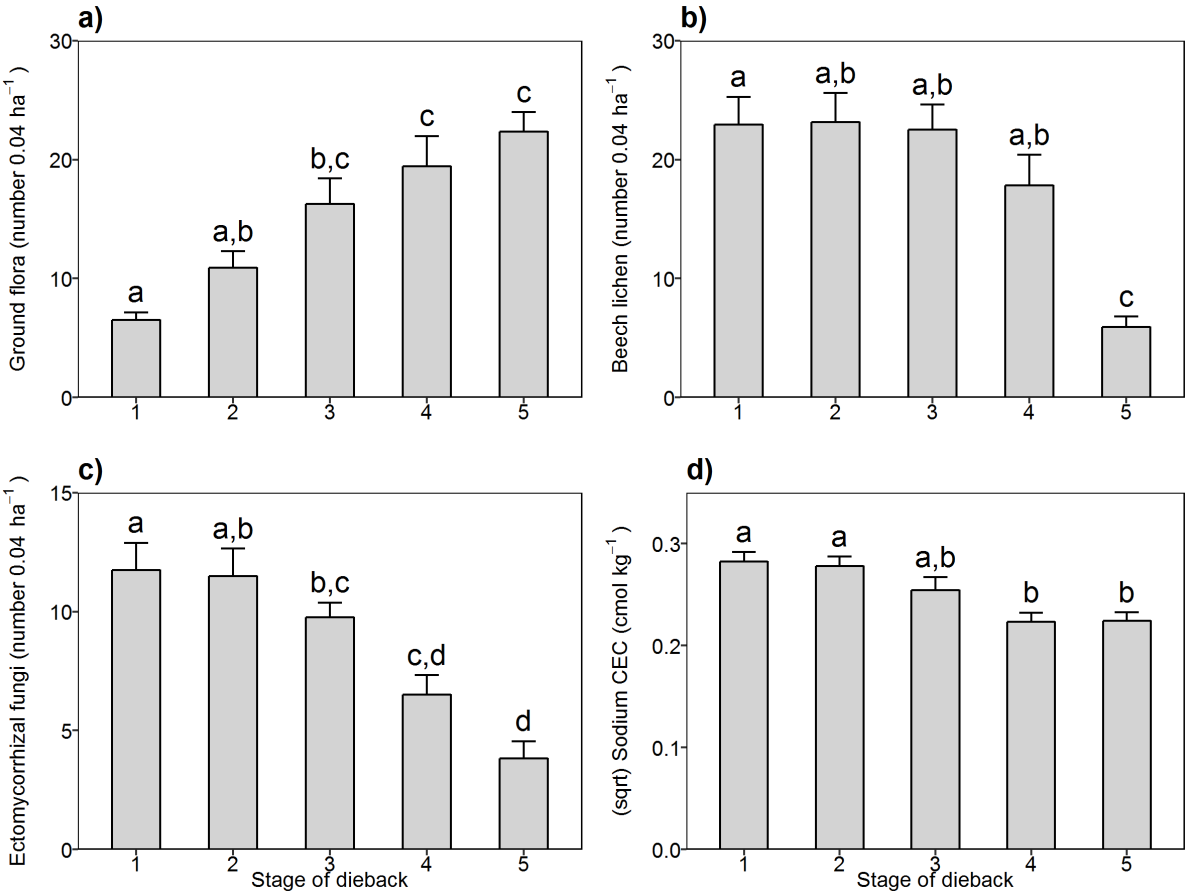

Fig. 3.5: Mean values of single-time assessment, ecological skill indicators (a, b and c) and a harder to record variable (d) measured across the stages of dieback: a, b, c, and d are ground flora richness, lichen richness on beech, ectomycorrhizal fungi richness and sodium CEC, respectively. The black bars indicate the standard error of the mean. Means grouped by the same letter are not significantly different ($p < 0.05$, Tukey HSD test). The units for all of the species richness measures shown here were number of unique species per 0.04 ha, the plot size.

3.5.2. Possible non-CSM indicators

None of the CSM condition targets specifically considered the basal area, stem density, tree structure or the biomass of trees, all of which are common measures of woodland condition (Angelstam and Dönz-Breuss, 2004; Newton, 2007; Cantarello and Newton, 2008; Gao et al. 2015; Trumbore et al. 2015). No metrics of other biodiversity measures were recorded either. Some of these measures were included in the assessment of non-CSM indicators, the results of which give support to the second hypothesis of this study, namely that some non-CSM indicators could be used to effectively determine different beech dieback stages.

3.5.2.1. Single-time, easy to assess indicators

Findings presented here indicate that there are some targets that could possibly be used in woodland CA, based on the value of the indicator differing significantly over at least two dieback stages. Concentrating specifically on indicators that do not require intensive field measurement or calculation (e.g. biomass and carbon storage), effective woodland condition indicators in this study were identified as beech biomass, sward height, canopy openness and the volume of lying dead wood. Beech biomass was very sensitive to beech dieback condition and declined further at every stage over the gradient, while lying dead wood increased positively with dieback stage. However, owing to the variability of dead wood, the Total dieback stage was the only significantly higher stage when compared to the other stages.

Dead wood volume and canopy openness increases have obvious links to dominant canopy tree mortality, as they are sure signs of dieback (Anderegg et al. 2013). Thus, it is unsurprising that these variables changed with dieback and were therefore good indicators of condition in terms of BA decline. Usefully, it has also been observed that both dead wood and canopy openness correlate to other biodiversity measures (Gao et al. 2014, 2015), making them important aspects of forest condition assessments (Noss, 1999; Hagan and Whitman, 2006; Rondeux and Sanchez, 2010). This is especially true for dead wood which provides habitats for many forest-dwelling species, including invertebrates (Jabin et al. 2004), lichen (Humphrey et al. 2002) and wood-inhabiting fungi (Nordén and Paltto, 2001; Penttilä et al. 2004). However, as pointed out by Rondeux and Sanchez (2010) in their review of commonly-used biodiversity indicators, dead wood is a useful measurement but differs more than other structural forest metrics; therefore it is complex to use it as an indicator without site-specific information first.

Interestingly, canopy openness, dead wood and sward height were included as part of the woodland CSM assessment. The difference is, however, that CSM used threshold target amounts and qualitative (i.e. subjective) assessments (JNCC, 2003) rather than quantitative values, which impacted the number of times these targets were met across the 12 study sites in this study. For example, CSM targets for dead wood and canopy openness were passed more times on the Major dieback than any other stage. This may affect their sensitivity as targets of woodland condition. Nonetheless, Legg and Nagy (2006) point out that quantitative monitoring methods are not always better than qualitative ones, especially when resources are limited. In fact, for rapid assessment of woodland condition, Bouget et al. (2014) found that large dead wood logs (diameter > 40 cm, length ≥ 1 m) were strong indicators of saproxylic beetle diversity, which would be

simple to identify visually. Further, they showed the same for standing dead wood (i.e. snags), but this is currently not in the woodland CSM targets.

3.5.2.2. Single-time assessment, ecological skill indicators

The single-time assessment variables that required ecological skills mostly pertained to biodiversity metrics including taxa identification, which are considered a key indicator of forest condition, forming part of the monitoring frameworks for forest health monitoring organisations (e.g. the ICP framework, Michel and Seidling (2016); EEA, 2012). Here, biodiversity that could be used as condition indicators include the species richness of epiphytic lichen and ECM, which declined over the gradient of dieback, and vascular ground flora and ground-dwelling arthropods, which increased positively with dieback. In agreement with the ECM finding, Treu et al. (2014) found that ECM species richness declined as the BA of lodgepole pine (*Pinus contorta* var. *latifolia*) also declined in Canada following a stand-destroying beetle attack.

Similar trends to the ground flora results from this study were observed in other floral diversity studies which focused on light gradients in European and North American forests (Tinya et al. 2009; Van Couwenberghe et al. 2011; Neufeld and Young, 2014; Sabatini et al. 2014). In all those studies, the availability of light was usually suggested as the reason for the increases in species richness, with light availability explaining about a third of the ground flora richness variance in beech forests (Sabatini et al. 2014). Similar results pertaining to ECM in this study were also found in other work. For example, Štursová et al. (2014) recorded fungal diversity and biomass over a temporal period, before and during bark beetle-induced dieback, and found that the microbial biomass of fungi in the soil declined as soon as dieback began. Furthermore, Heilmann-Clausen et al. (2014) showed that fungi are highly affected by environmental change, albeit saproxylic fungi rather than ECM, causing the species richness to decrease. Interestingly, that study determined that the forest condition (including naturalness, dominant tree age and forest cover) was responsible for explaining 20% of the variance, while climate factors and substrate quality explained 21% and 23%, respectively, which shows that different aspects need to be included in condition assessments.

Although the biodiversity metrics obtained in this study are potentially useful indicators, owing to the fact they differed between some stages, none of them differed between every dieback stage. Thus, one biodiversity indicator on its own may not be enough. However, as shown in this study and others, ECM and ground flora species richness exhibit negative and positive trends with dieback, respectively. Therefore, using

combination measures of the two taxa over the gradient in assessments may help to detect the changing condition of woodlands (Gao et al. 2015).

3.4.2.3. Harder to record and measure indicators

The harder to record indicators in this study related mainly to soil properties, which are often neglected when taking measurements of ecosystem functioning (Lavelle et al. 2006). Some of the soil properties changed with dieback and thus could be used as indicators of condition. Independent of other variables which may affect soil chemistry, it was found that both the soil sodium and calcium CEC varied across the dieback gradient, with calcium increasing two-fold and sodium decreasing about one-third between the Intact and Total dieback stages. Conversely, other studies have found that soil calcium concentration correlates negatively with forest age (Hamburg et al. 2003) and soil N percentage (Perakis et al. 2013). Similarly, Prober et al. (2002) noted that Ca increased with tree cover in eucalyptus forests. However, these studies all focused on disparate woodland types and not over a gradient of condition degradation.

The soil respiration rate was another attribute that showed significant variation, decreasing by approximately a third between its highest and lowest points, the Intact and Major dieback stages, respectively. The data generally disagreed with other studies on soil respiration which focused on woodland to grassland transitions and comparisons (e.g. Kaye and Hart, 1998; Smith and Johnson, 2004). This difference could possibly be explained due to the fact that soil respiration in different beech stands can be very variable (Priwitzer et al. 2013) and rates are reliant on many other factors including soil moisture and temperature (Smith and Johnson, 2004). Thus, while the soil attributes measured here could be used as indicators of condition, more work would need to be done beforehand to make sure they are appropriate for the particular woodland of interest.

3.5.3. Beech dieback and woodland condition

In this Chapter, the underlying assumption was that the stage of beech dieback was synonymous with the overall condition of the woodland. However, this may not necessarily hold true, depending on which aspect of forest condition is favoured or being tested – beech dieback is only one specific aspect of woodland condition. For example, foresters often use stand level productivity as a measure of condition, which was not included in the indicators used in this study. Moreover, although there is a main focus on beech in this work, the ideal forest conditions for other biodiversity may not follow the same trajectory, relating to other flora or fauna. Also, as stated by Edmonds et al. (2000),

forest condition assessments may have to include human needs, which are many and varied, and need to include spatial and successional variation. This is just a selection of other metrics that have been used in assessing woodland condition; therefore, the results of this Chapter need to be interpreted with care, and other indicators of forest condition should also be considered in that interpretation. Overall, indicators of forest condition should be considered in the context of whole stand development, recruitment, growth and regeneration when focusing on forest health (Luo and Chen, 2013; Trumbore et al. 2015).

3.6. Conclusions and usefulness for inferring resilience

This study found that although the current overall CSM CAs are not adequate to determine the stage of dieback, there are several indicators that could be used successfully over a dieback gradient, to determine relative condition. For this purpose, possible diverse indicators were highlighted, which are needed for any comprehensive woodland CAs (Ferris and Humphrey, 1999; Noss, 1999; Gao et al. 2015). From this study, potential indicators include: easy-to-collect indicators of dead wood volume, canopy openness, and sward height; species richness measures of ground flora, ectomycorrhizal fungi, epiphytic lichen and possibly ground-dwelling arthropods; and soil measurements of calcium and sodium, and soil respiration rate. Adoption of these metrics could enable rapid adaptive management and adjustment to plans (as detailed in JNCC (2003), for example) for the purpose of continuing to maximise ecosystem goods and services (Temperli et al. 2012), and effective biodiversity conservation (Westgate et al. 2013) in SSSIs.

From the results of the CSM CAs, it is clear that none of the target lists changed monotonically with the forest dieback condition, as is required for resilience assessment surrogates (Carpenter et al. 2001), when condition was based on BA decline. Therefore, CSM CAs could not be used effectively in resilience assessments to infer the current state of resilience of a particular stand (Carpenter et al. 2001; Bennett et al. 2005; Nemec et al. 2014). Similar is true for the other indicators tested in this Chapter, as none of them, with the exception of beech biomass, changed significantly in a systematic way (i.e. negatively or positively) with condition.

Chapter 4:
Evaluation of the use of airborne lidar in detecting forest condition

4.1. Abstract

Woodland ecological indicators are needed to assess and detect changing habitat condition, as a basis to inform conservation management and infer resilience. The use of suitable indicators is increasingly pertinent in a rapidly-changing world as monitoring this change will require greater data collection and faster analysis. This is especially true for ecosystems which are particularly vulnerable to change such as for old-growth woodlands. In this study, lidar-derived forest structure variables were tested against field-collected habitat condition indicators to explore whether any relationships existed between the two. The purpose was to determine how useful variables obtained from airborne lidar, a relative inexpensive and rapid data collection tool, would be as surrogate measures for other attributes of habitat condition. Specifically, the hypotheses tested were: i) biodiversity; ii) stand condition; iii) herbivore damage; and iv) soil condition could be predicted by lidar-derived structural measures. The main results of this study indicated that some lidar-derived structural measures could potentially be used to predict other woodland condition values, especially ground flora species richness. However, a majority of the other habitat condition indicators could not be predicted using lidar metrics, which may limit the application of lidar to infer habitat condition.

4.2. Introduction

Large-scale, rapid degradation of forests is becoming more common globally due to increases in abiotic and biotic threats (Hansen et al. 2013; Allen et al. 2015). Degradation is further exacerbated by human means, through both direct and indirect interactions, major consequences of which include: an increase in the rate of biodiversity loss, which can modify ecosystem service provision due to ecosystem productivity declines (Isbell et al. 2013); a reduction in the carbon storage potential of forests; major modifications to soil properties (Hajabbasi et al. 1997; Haque et al. 2014); and a decrease in the condition of surrounding woodland patches (Curran et al. 1999; Broadbent et al. 2008), which often produces a positive feedback, leading to greater simplification of habitat structure.

Forest degradation is especially detrimental for old-growth woodlands, as they are habitats that are crucial and often irreplaceable for vast amounts of biodiversity (Gibson

et al. 2011). Of all forest cover in Europe, which is approximately 44% of the land area with the inclusion of the Russian Federation or 32% with its exclusion (Forest Europe, UNECE and FAO, 2011), only 0.2% of the European deciduous woodlands are old-growth forest (Hannah et al. 1995; Frank et al. 2009). Despite this low amount, degradation of these ancient forests is continuing, and therefore their extent is being further reduced (Knorn et al. 2013; Martin et al. 2015). For this reason, rapid, accurate assessments of forest condition are needed to help inform management of old-growth forests for the purposes of conservation and maintenance of resilience (Trumbore et al. 2015).

Remote sensing – the acquisition of information via non-contact recording methods (Jones and Vaughan, 2010), is one tool that is increasingly being used in ecological assessments to decrease the time (and other resources) needed to collect ecological data, which can include data that would be inaccessible from field studies (Pettorelli et al. 2014). Remote sensing is a relatively cheap method that enables continual mapping and monitoring of broad-scale habitats, as well as the production of biodiversity inference and prediction tools, such as species distribution models (Aplin, 2005; Newton, 2007; Pettorelli et al. 2014). It also has the potential to contribute to machine learning, making conservation efforts more streamlined and assessments quicker (Gleason and Im, 2012; Moran et al. 2017).

Airborne lidar – a scanning laser used to measure the distance between an aircraft and different surfaces by capturing the echoes of reflected lasers, is one remote sensing method that has gained a lot of use in answering ecological questions (Turner et al. 2003), especially for woodlands research (Zellweger et al. 2014; Hill and Hinsley, 2015). In forests, the surfaces that lasers rebound off include stems, branches and foliage from the top of canopy to the forest floor, thus the output represents the 3d structure of a forest (van Leeuwen et al. 2008), and has the capacity to provide highly accurate information for forest surveys (Tinkham et al. 2012; Sumnall et al. 2016). Such data would be resource heavy to measure using ground-based methods (Pettorelli et al. 2014).

Lidar-derived structural measures such as canopy cover, tree diameter and height, tree height percentiles, percentage cover of different strata (e.g. understorey, overstorey), tree spacing, tree species, stand biomass, understorey vegetation and dead wood have proved informative in this way for ecological studies (Zellweger et al. 2014; Hill and Hinsley, 2015). Ecology-focused remote sensing has recently been used to determine relationships between forest structural variables and species richness of plants (van Ewijk et al. 2014; Higgins et al. 2014; Lopatin et al. 2016), birds (Garabedian et al. 2014; Hill

and Hisley, 2015; Coops et al. 2016), lichens (Korpela, 2008), mammals and invertebrates (Müller and Brandl, 2009; Fergnani et al. 2010; Levanoni et al. 2011); deforestation and land-clearance (Ghebrezgabher et al. 2016); biomass estimation and carbon storage (Asner et al. 2012; Ene et al. 2016); and for measuring the impacts of fire in a pine savannah (Listopad et al. 2015).

In the same way, lidar could potentially be used to infer the ecological habitat condition as a basis for monitoring and informing management decisions for conservation (Hill et al. 2014; Simonson et al. 2014). As defined by Noss (1990), there are three primary attributes of woodland ecosystems that can indicate its habitat condition for biodiversity: structure, function and composition, all three of which are related. From the results of Chapter 2, it is shown that there are relationships between woodland structure, biodiversity and function. Thus, when structure changes (tree dieback, in Chapter 2), biodiversity and ecosystem functioning change as well. This has been further evidenced by Martin et al. (2015) in a temporal context, showing that ground flora species richness and grass cover increased in response to tree dieback; and by Gao et al. (2014), who showed that structural inventory data can be used to predict forest biodiversity. Some of the ways forest structure influences condition is by providing layering and allowing light in to create different habitats for other life such as trees, shrubs, grasses, and different fauna, whereas soil structure and condition (e.g. nutrient content) can impact the growth and survival of trees. Therefore, as forest structure is related to the provision of habitat for different species and other forest functions and conditions, lidar-derived structural data may be able to be used to infer overall habitat condition and thus inform management (Lawley et al. 2016).

One of the knowledge gaps that is under-examined is whether remote sensing applications can be accurately used in detecting forest condition of different ecosystem properties, especially different taxa (Hill et al. 2014). In this way, lidar could be a highly effective conservation tool and contribute to habitat condition assessment at the stand or landscape scale (Hill et al. 2014). Such knowledge is important when considering disturbance dynamics, growth stages, woodland ecosystem processes, forest health and condition, and wildlife habitats (Maltamo et al. 2005; Hill and Hinsley, 2015; Trumbore et al. 2015). The objective of this study was therefore to test whether lidar-derived structural measures could be used as surrogates for other indicators of forest condition. As shown in the Chapter 2 of this thesis, relationships may not be linear; therefore, non-linear relationships were examined as well. Specifically, the hypotheses that i) biodiversity (vascular ground flora, ectomycorrhizal fungi (ECM), tree seedling richness

and abundance), ii) stand condition (leaf loss, structural crown loss, crown discolouration and overall crown condition (i.e. crown dieback), iii) herbivore damage (dung and browseline) and iv) soil condition (percentage of C and N in the soil and the C:N ratio) could be predicted by lidar-derived structural measures were tested.

4.3. Materials and methods

4.3.1. Study site

This study was conducted in the Denny Wood area of the New Forest. In-depth details of the site can be found in Mountford et al. (1999), Mountford and Peterken (2003) and Martin et al. (2015), with some of the more important features presented here. The site has historically been dominated by European beech (*Fagus sylvatica*), with a frequent presence of pedunculate oak (*Quercus robur*), occasional birch (*Betula pubescens* and *B. pendula*), and a dense understorey composed mostly of holly (*Ilex aquifolium*). Soils are acidic (pH 3.5 – 5), with a majority being brown earth clay, but there are localised sandier soils. The study site has not been managed in terms of silviculture, and in 1870 it was divided into two sections through the creation of an enclosure, the aim of which was to reduce browsing pressure on the enclosed portion of the site.

A 1 km x 20 m transect is present in the enclosed portion, and a shorter, perpendicular transect (320 m x 20 m) is found on the unenclosed portion (Fig. 4.1). Both transects have been repeatedly assessed over the last 50 years, giving unique insight into how change has occurred (Martin et al. 2015). Both transects were split into 20 x 20 m (0.04 ha) plots. All data for this study were obtained from these two transects. In the longer transect, two plots were not recorded due to previous direct, disruptive management that had altered the composition and sturucture of the plots, which was not included in the aim of this study; therefore, those plots were ignored.

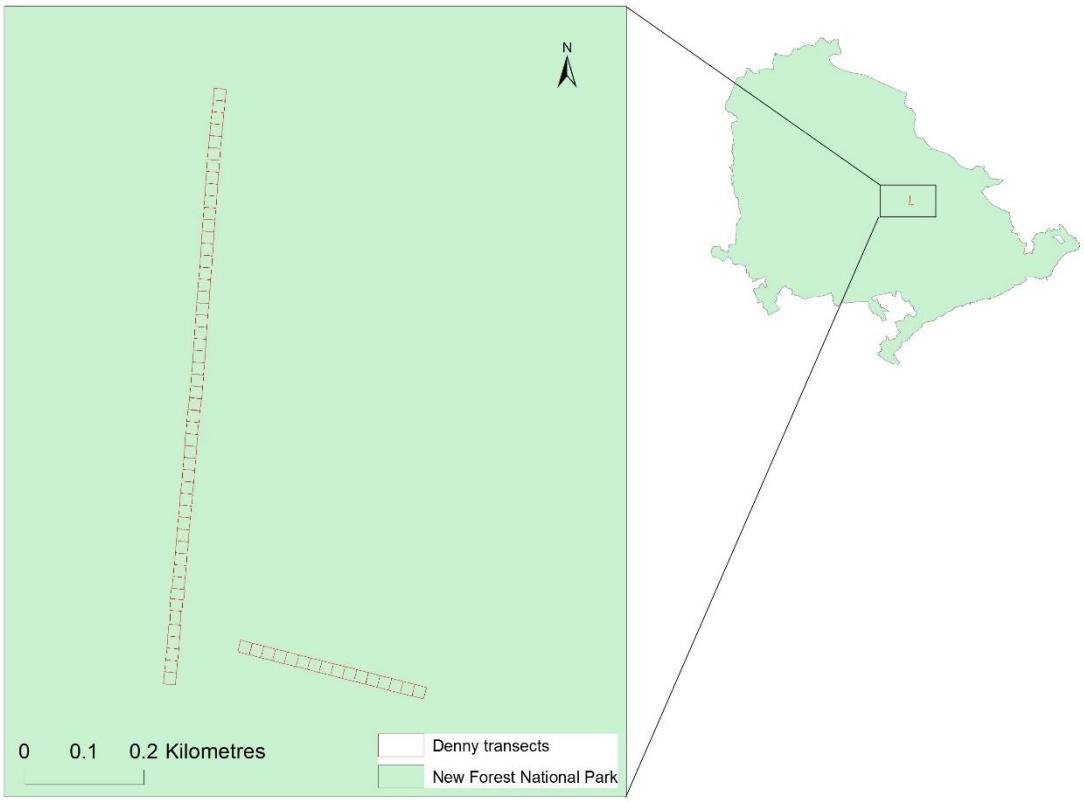

Fig. 4.1: Map of the two transects in Denny Wood, New Forest.

4.3.2. Study design

Airborne lidar data and field-collected habitat condition data were obtained from the study site to explore whether lidar-derived structural metrics could be used to predict habitat condition and therefore be used as suitable indicators of forest ecological condition in remote sensing assessments in the future.

4.3.3. Field data collection

Field-collected metrics of biodiversity, stand condition, soil condition and herbivore damage were collected for this study. The field-collected variables were chosen as they all relate to ecological condition. Biodiversity is the most widely-used indicator of woodland ecological condition owing to its ease of assessment for forest researchers (Ferris and Humphrey, 1999) and because a rich diversity of species is considered important for the health of forests and people, partly through the ES they provide (Diaz et al. 2006; Mace et al. 2012). Stand condition metrics pertained to structure and functions associated with trees in the stand, focusing specifically on crown condition [of trees in the stand]. These were direct measurements of forest ecological condition (Eichhorn et al. 2010). Soil condition has influence on the growth and survival of flora within woodlands and plays a key role in the hydrological, carbon and nutrient cycles of forests.

In fact, nutrient cycling underpins all other functions by cycling chemical elements between the biotic and abiotic components (Wardle et al. 2004; MEA, 2005). Finally, herbivore damage, specifically ungulates, can impact the condition of a forest by damaging plants and preventing regeneration (Brown, 1953; Vázquez, 2002). All the specific metrics used can be found in Table 4.1.

Biodiversity field data collection focused on surveys of different taxa, namely herbs (herein known as ground flora), ectomycorrhizal fungi (ECM), and woody tree seedlings separately. The abundance of seedlings was also recorded. The plant surveys took place over the summer of 2014. ECM richness was recorded in winter 2014, with all of the plots being assessed over a period of two days, using expert sporocarp identification.

Soil was collected from five points in each plot (one in the centre, and four from the exact points halfway between the corners and the centre) for the purpose of analysing the carbon and nitrogen content as a proportion of the total soil volume. The top 15 cm of the mineral soil was extracted using a 10-cm diameter auger, which was hammered into the ground at an angle flush to the top of the soil. Bulk density was collected using 4.5 cm diameter by 4.5 cm deep (72 cm^3) cores. Soil samples from each plot were placed into the same bag for N and C content analysis, and a separate bag for the bulk density analysis. All soil was sent to the Forest Research laboratory at Alice Holt to be analysed for total C, total N, bulk density and particle size analysis. Soil analysis followed laboratory protocols: ISO standards 10694:1995 and 13878:1998 for C and N; ISO 11272:1998 for bulk density; and laser diffraction for particle size analysis (silt, sand and clay content). The quantity of dung, structural crown loss, leaf loss, discoloration and crown condition were recorded as in Chapter 2.

Table 4.1: Field-collected variables of the habitat condition measures used in this study. HD and BD indicate that the variable was collected as an indicator of herbivore damage and biodiversity, respectively.

Metric Name	Units	Condition indicator type	Metric Description
Bulk Density (BD)	g cm^{-3}	Soil	Weight of soil for a known volume
Browseline	%	HD	Percentage of the bottom of tree crowns above 1.8 m

Clay	%	Soil	Percentage of 0-2 µm sized particles in the soil
CN Ratio	Ratio of C to N	Soil	The ratio of carbon to nitrogen in the soil
Crown condition	1-5 scale (see Chapter 2 methods)	Stand	Overall crown condition of living trees in the plot, based on a 1-5 scale
Crown loss	%	Stand	Percentage structural loss of the living crowns of the plot compared to their potential fulfilment of space
Deer dung	Number pellets per 0.04 ha divided by pellet condition (see Chapter 2 methods)	HD	Adjusted number of deer dung pellets per plot
Discolouration	%	Stand	Percentage of present leaves in the living crowns of the plot that are discoloured
Fungi richness	Number unique species per 0.04 ha	BD	Number of unique ectomycorrhizal fungi species per plot
Ground flora richness	Number unique species per 0.04 ha	BD	Number of unique ground flora species per plot
Leaf loss	%	Stand	Percentage leaf loss of the living crowns of the plot compared to their potential fulfilment of space

Pony dung	Number pellets per 0.04 ha divided by pellet condition (see Chapter 2 methods)	HD	Adjusted number of pony dung pellets per plot
Sand	%	Soil	Percentage of 63 µm-2 mm sized particles in the soil
Tree seedling abundance	Number of individuals per 0.04 ha	BD	Number of individual tree seedlings per plot
Tree seedling richness	Number unique species per 0.04 ha	BD	Number of unique tree seedling species per plot
Silt	%	Soil	Percentage of 2-63 µm sized particles in the soil
Soil carbon	%	Soil	Percent of carbon in the soil
Soil nitrogen	%	Soil	Percent of nitrogen in the soil

4.3.4. Airborne lidar data acquisition and pre-processing

Discrete return airborne lidar data for Denny Wood were acquired in July 2010 and were provided by the Airborne Research and Survey Facility, a division of the Natural Environment Research Council, in a point cloud format with X, Y and Z coordinates. The point cloud was processed by, and is fully described in, Sumnall (2013), with only important information described here. The lidar data were recorded as leaf-on (i.e. recorded at a time when trees were in leaf) using a Leica ALS50-II airborne laser scanner. The maximum pulse rate was 83 KHz, with up to four returns from each discrete laser pulse. To ensure that lidar data and ground data were geographically accurate, the mid-points of the transect plots were mapped to a high precision using a differential GPS and Total Station (Leica Viva TS11; Leica Geosystems AG) with an accuracy of up to 2 cm.

Similarly, the position of the lidar aircraft was mapped using a differential GPS, with a maximum error of 11 cm (Leica Geosytems, 2003). For more detailed information about technical specifications of the lidar data and collection, see Sumnall (2013) and Table 4.2. It should be noted that there was a 4-year time difference between lidar acquisition and field data collection.

Table 4.2: Lidar data acquisition characteristics used in this study.

Acquisition Parameter	
Scanner	Leica ALS50-II
Wavelength	5700 ft
Flying altitude	*ca.* 1600 m
Flying date	July 2010
Pulse repetition frequency	83 KHz
Scan half angle	10°
Maximum returns per pulse	4
Point density	3.7 pulses per m^2

4.3.5. Lidar data collection

From the differential GPS data, outlines of each transect plot were delineated using ArcGIS 10.1. Overall, 66 20 x 20 m plots were used. No plots overlapped, but they were adjacent (Fig. 4.1). The structural lidar data were processed directly from a height normalised point cloud, which was treated as a single data set, as described in Sumnall (2013).

Overall, 22 variables were extracted from the lidar point cloud, 11 each for both the first return (FR) and all returns (AR) point clouds. A range of lidar-derived variables were used to capture the important structural features of woodland, namely the height, canopy structure and different types of vegetation cover. The maximum height (MH), which was the same for both AR and FR, average height (AH), and the height percentiles (H50 and H95) of the lidar returns were calculated from the first returns of the point cloud data in a plot. Vegetation cover was measured as the amount of returns from 0.5 – 2 m, 2 – 5 m, and >5 m for ground cover (Ground), understorey (Under) and overstorey (Over), respectively. The cut-off of 5 m for the understorey was used based on average height measurements taken directly from both transects, recorded using a clinometer (see Chapter 2 methods). Canopy closure (CC) was measured as the percentage of returns above a canopy height threshold of 2 m, the average height of the lower canopy line in

Denny Wood. Vegetation distribution ratio (VDR) was used as a proxy for the depth and continuity of canopy, which is used in development stage indication (Franklin et al. 2002) and measured as the ratio between MH and H50. Canopy permeability (CP) was recorded as the proportion of laser pulses for which there were multiple returns. For a full list of lidar-derived metrics used, see Table 4.3.

Table 4.3: Lidar-derived structural metrics taken from the 2010 lidar point cloud data. These metrics were derived separately using both all returns (AR) and only the first returns (FR).

Metric Name	Abbreviation	Metric Description
H_max	MH	Maximum height (m)
H_mean	AH	Average height (m)
H_std	SDH	Standard deviation of canopy height (homogeneity of the canopy)
H_50	H50	Median height (m)
H_95	H95	95% height percentile (m)
Canopy permeability (for FR)	CP	Proportion of first returns with a secondary return
Canopy permeability (for AR)	CP	Proportion of all returns that are secondary returns
Canopy closure	CC	Percentage of returns above a canopy height threshold of 2 m
Ground	Ground	Percentage of returns in the ground layer (i.e., 0.5-2 m)
Understorey	Under	Percentage of returns in the understorey layer (i.e., 2–5 m)
Overstorey	Over	Percentage of returns in the overstorey layer (i.e., >5 m)
Vegetation distribution ratio	VDR	Vegetation distribution ratio (H_max-H_50/H_max)

4.3.6. Statistical analysis

Initially, the data were analysed using Pearson correlations to determine whether any relationships existed between lidar-derived variables and field-collected variables. The

field-collected data obtained from the two transects were compared and analysed using one-way ANOVAs to determine whether the values significantly differed between the two transects (see Appendix 4.3).

Generalised linear regression models (GLMs) were used to determine if relationships between the lidar and field-collected variables existed. GLMs were used as they correct for different data structure (e.g. count data) and as they can predict non-linear relationships. GLMs have been shown to be suitable for analysing lidar and field data together (Lopatin et al. 2016). For count data (species richness and abundance), initially a Poisson error distribution was used as the data were all non-negative integers (ver Hoef and Boveng, 2007). However, as is common with ecological data, a lot of the models were 'over-dispersed' (i.e. the variance was greater than the mean), as determined by the *dispersiontest* function in the AER R package (Cameron and Trivedi, 1990; Kleiber and Zeileis, 2016). Models that presented overdisperion were consequently refit with quasi-Poisson and negative binomial distributions, which are two of the most common methods to deal with this problem (see Appendix 4.1 for more information). To choose the most appropriate modelling distribution between the Poisson, quasi-Poisson and negative binomial distributions, the *odTest* from the *psc1* R package (Jackman, 2015) was used. The occurrence of over-dispersed data in ecology is often due to a lack of independence among the plots (Eberhardt, 1978; Cox and Snell, 1989), especially spatial autocorrelation. To test whether spatial autocorrelation was significant in each GLM, Moran's I was calculated following the spatial generalised linear mixed model method, as described in Dormann et al. (2007). If it was, a corrective spatial term was included in the GLM.

Soil C and N were measured as percentage of the soil, therefore the analysis that was required was beta regression (BR), based on a beta distribution response, as the values were restricted to 0 and 100. BR allows easier interpretation and more accurate inference of percentage data results, and deals with asymmetry in the data distribution, as is normally the case with proportion or percentage data (Ferrari and Cribari-Neto, 2004).

Three models were tested for each response (field-collected) variable: a null model, a model with linear form of the predictor (the lidar-derived variable), and a model with the quadratic form of the predictor. Both AIC and r^2 values were calculated for all models, to provide information on the optimal model and the goodness-of-fit of the modelled data, respectively. AIC was used for model selection corrected for small samples sizes, following Burnham and Anderson (2002). For species data, r^2 was calculated following McFadden (1974), a calculation based on the deviance of the model

residuals. The r^2 for percentage soil data was calculated as the square of the sample correlation coefficient, from the *betareg* package (Zeileis et al. 2016), as a beta distribution was used (Cribari-Neto and Zeileis, 2010). Each combination of response and predictor were tested up to three times, with data from each transect analysed separately and subsequent analysis of data from both transects combined. Seven of the field-collected variables were only collected in the longer transect, and thus only analysed once. The rest of the variables were recorded in both transects. All analyses were performed in R 3.1.2. (R Development Core Team, 2011, http://www.R-project.org). A relationship was considered to be substantial if it met two *a priori* criteria relating to the most parsimonious model: 1) its ΔAICc was ≥ 4 compared to the null model; and 2) its r^2 value was > 0.4.

These criteria were defined *a priori*, before conducting the analysis, to ensure a degree of rigour and objectivity in the detection of relationships. It should be noted that the criteria were developed by myself, based on what is considered to be consistent with good practice, as described by Burnham and Anderson (2002). The *a priori* criteria differ slightly from Chapter 2 for two reasons: 1) the data were used to determine whether one variable could be used to predict another, therefore, a higher r^2 value was required compared to the detection of a trend; and 2) ΔAICc was compared to the null model in this Chapter, rather than the next closest model, therefore, a greater ΔAICc was required to make sure there was enough distinction from the null model.

4.4. Results

Overall, 22 lidar-derived variables (11 AR and 11 FR) were tested individually against 18 field-collected ecological condition variables to see whether the lidar-derived variables could be used as a proxy for forest condition.

4.4.1. Correlations between lidar and field-based metrics

There were numerous significant correlations between the lidar-derived variables and field-collected data, where correlations were classed as significant at the Bonferroni-adjusted alpha level of 0.005, to account for type I errors (i.e. false positives). This was particularly noticeable relating to the soil conditions and biodiversity, whereas the stand condition field-based metrics and the herbivore damage variables had fewer significant correlations.

For the soil conditions metrics, the soil structure variables, namely clay, silt and sand soil content were significantly correlated with most of the lidar-derived variables

(Table 4.4). The strongest correlations with the soil structure variables were FR overstorey development ($p < 0.001$, r = -0.428, -0.487 and 0.507 for clay, silt and sand, respectively), FR canopy closure ($p < 0.001$, r = -0.450, -0.484 and 0.519) and FR ground ($p < 0.001$, r = 0.408, 0.420 and -0.462).

The most highly correlated biodiversity metrics were ground flora richness and seedling richness (Table 4.5). With the exception of AR standard deviation of canopy height, Ground flora species richness had significant relationships to all lidar-derived metrics, the strongest correlations of which were with AR average height (r = -0.666, $p < 0.001$), FR overstorey (r = -0.651, $p < 0.001$) and AR canopy closure (r = -0.598, $p < 0.001$). Similarly, seedling richness exhibited the strongest significant correlations with FR average height (r = -0.568, $p < 0.001$) and FR canopy closure (r = -0.564, $p < 0.001$).

For the herbivore damage variables (Table 4.6), pony dung correlated significantly with lidar metrics of FR SD height (r = 0.290, p = 0.005) and FR understorey (r = 0.323, p = 0.001), and deer dung correlated significantly with understorey (r = 0.377, $p < 0.001$/ r = 0.394, $p < 0.001$ (FR/AR)). The stand condition field-based metrics did not correlate with the lidar-derived variables at all (Table 4.6).

Table 4.4: Pearson correlation results between field-based soil condition measures for both transects from 2014 and lidar-derived metrics from 2010 lidar point cloud data. Values shown in bold are considered are significant to the alpha level of 0.005.

Lidar-derived variable	All returns (AR) or first return (FR)	Clay		Silt		Sand		Total nitrogen		Total carbon		CN ratio	
		r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
Max.Height	FR	**-0.123**	**0.005**	**-0.332**	**<0.001**	**0.24**	**<0.001**	**0.315**	**<0.001**	**0.286**	**<0.001**	-0.038	0.396
Ave.Height	FR	**-0.384**	**<0.001**	**-0.482**	**<0.001**	**0.477**	**<0.001**	**0.226**	**<0.001**	**0.33**	**<0.001**	**0.166**	**<0.001**
SD.Height	FR	**0.369**	**<0.001**	**0.265**	**<0.001**	**-0.361**	**<0.001**	-0.004	0.935	**-0.15**	**0.001**	**-0.182**	**<0.001**
H95	FR	**-0.161**	**<0.001**	**-0.405**	**<0.001**	**0.3**	**<0.001**	**0.338**	**<0.001**	**0.327**	**<0.001**	0.002	0.97
H50	FR	**-0.283**	**<0.001**	**-0.415**	**<0.001**	**0.381**	**<0.001**	**0.266**	**<0.001**	**0.318**	**<0.001**	0.113	0.011
Canopy.perm	FR	**-0.325**	**<0.001**	**-0.171**	**<0.001**	**0.287**	**<0.001**	0.067	0.129	**0.237**	**<0.001**	**0.272**	**<0.001**
Can.Closure	FR	**-0.45**	**<0.001**	**-0.484**	**<0.001**	**0.519**	**<0.001**	**0.184**	**<0.001**	**0.317**	**<0.001**	**0.197**	**<0.001**
Ground	FR	**0.408**	**<0.001**	**0.42**	**<0.001**	**-0.462**	**<0.001**	**-0.159**	**<0.001**	**-0.285**	**<0.001**	**-0.194**	**<0.001**
Understorey	FR	**0.16**	**<0.001**	**0.286**	**<0.001**	**-0.241**	**<0.001**	**-0.244**	**<0.001**	**-0.245**	**<0.001**	-0.045	0.308
Overstorey	FR	**-0.428**	**<0.001**	**-0.487**	**<0.001**	**0.507**	**<0.001**	**0.218**	**<0.001**	**0.334**	**<0.001**	**0.182**	**<0.001**
VDR	FR	**0.291**	**<0.001**	**0.389**	**<0.001**	**-0.374**	**<0.001**	**-0.242**	**<0.001**	**-0.303**	**<0.001**	**-0.125**	**0.005**
Max.Height	AR	**-0.123**	**0.005**	**-0.332**	**<0.001**	**0.24**	**<0.001**	**0.315**	**<0.001**	**0.286**	**<0.001**	-0.038	0.396
Ave.Height	AR	**-0.371**	**<0.001**	**-0.47**	**<0.001**	**0.464**	**<0.001**	**0.258**	**<0.001**	**0.355**	**<0.001**	**0.16**	**<0.001**
SD.Height	AR	**0.226**	**<0.001**	0.008	0.859	**-0.146**	**0.001**	**0.17**	**<0.001**	0.058	0.187	-0.114	0.01
H95	AR	**-0.158**	**<0.001**	**-0.401**	**<0.001**	**0.296**	**<0.001**	**0.335**	**<0.001**	**0.324**	**<0.001**	0.002	0.969
H50	AR	**-0.311**	**<0.001**	**-0.43**	**<0.001**	**0.406**	**<0.001**	**0.26**	**<0.001**	**0.325**	**<0.001**	0.12	0.007
Canopy.perm	AR	**-0.362**	**<0.001**	**-0.24**	**<0.001**	**0.345**	**<0.001**	**0.124**	**0.005**	**0.309**	**<0.001**	**0.3**	**<0.001**
Can.Closure	AR	**-0.446**	**<0.001**	**-0.458**	**<0.001**	**0.504**	**<0.001**	**0.167**	**<0.001**	**0.301**	**<0.001**	**0.195**	**<0.001**
Ground	AR	**0.395**	**<0.001**	**0.382**	**<0.001**	**-0.435**	**<0.001**	**-0.138**	**0.002**	**-0.262**	**<0.001**	**-0.189**	**<0.001**
Understorey	AR	**0.167**	**<0.001**	**0.243**	**<0.001**	**-0.224**	**<0.001**	**-0.218**	**<0.001**	**-0.196**	**<0.001**	-0.024	0.595
Overstorey	AR	**-0.434**	**<0.001**	**-0.46**	**<0.001**	**0.498**	**<0.001**	**0.194**	**<0.001**	**0.31**	**<0.001**	**0.181**	**<0.001**
VDR	AR	**0.321**	**<0.001**	**0.409**	**<0.001**	**-0.402**	**<0.001**	**-0.24**	**<0.001**	**-0.312**	**<0.001**	**-0.129**	**0.004**

Table 4.5: Pearson correlation results between field-based biodiversity condition measures for both transects from 2014 and lidar-derived metrics from 2010 lidar point cloud data. Values shown in bold are considered are significant to the alpha level of 0.005.

Lidar-derived variable	All returns (AR) or first return (FR)	Ground flora richness		ECM richness		Seedling richness		Seedling abundance	
		r	*p*	*R*	*p*	*r*	*p*	*r*	*p*
Max.Height	FR	**-0.595**	<0.001	0.077	0.083	**-0.465**	<0.001	0.056	0.201
Ave.Height	FR	**-0.645**	<0.001	0.036	0.426	**-0.568**	<0.001	0.017	0.701
SD.Height	FR	**0.263**	<0.001	0.077	0.086	**0.201**	<0.001	0.017	0.694
H95	FR	**-0.59**	<0.001	0.05	0.26	**-0.51**	<0.001	0.018	0.677
H50	FR	**-0.627**	<0.001	0.063	0.156	**-0.525**	<0.001	0.076	0.085
Canopy.perm	FR	**-0.295**	<0.001	0.115	0.01	**-0.166**	<0.001	**0.332**	<0.001
Can.Closure	FR	**-0.623**	<0.001	**0.14**	**0.002**	**-0.564**	<0.001	0.089	0.044
Ground	FR	**0.535**	<0.001	-0.126	0.005	**0.552**	<0.001	-0.051	0.25
Understorey	FR	**0.442**	<0.001	0.045	0.313	**0.27**	<0.001	0.021	0.638
Overstorey	FR	**-0.651**	<0.001	0.11	0.014	**-0.558**	<0.001	0.073	0.098
VDR	FR	**0.597**	<0.001	-0.083	0.064	**0.517**	<0.001	-0.082	0.062
Max.Height	AR	**-0.595**	<0.001	0.077	0.083	**-0.465**	<0.001	0.056	0.201
Ave.Height	AR	**-0.666**	<0.001	0.029	0.514	**-0.561**	<0.001	0.053	0.23
SD.Height	AR	-0.099	0.023	0.118	0.008	-0.092	0.036	0.052	0.238
H95	AR	**-0.582**	<0.001	0.036	0.422	**-0.512**	<0.001	0.003	0.943
H50	AR	**-0.628**	<0.001	0.049	0.274	**-0.547**	<0.001	0.042	0.336
Canopy.perm	AR	**-0.419**	<0.001	**0.132**	**0.003**	**-0.235**	<0.001	**0.367**	<0.001
Can.Closure	AR	**-0.598**	<0.001	0.116	0.009	**-0.553**	<0.001	0.078	0.076
Ground	AR	**0.493**	<0.001	-0.095	0.033	**0.534**	<0.001	-0.032	0.469
Understorey	AR	**0.373**	<0.001	0.114	0.011	**0.247**	<0.001	0.055	0.21
Overstorey	AR	**-0.617**	<0.001	0.082	0.064	**-0.551**	<0.001	0.06	0.17
VDR	AR	**0.606**	<0.001	-0.068	0.126	**0.541**	<0.001	-0.052	0.24

Table 4.6: Pearson correlation results between field-based stand condition and herbivore damage measures for both transects from 2014 and lidar-derived metrics from 2010 lidar point cloud data. Values shown in bold are considered are significant to the alpha level of 0.005.

Lidar-derived variable	All returns (AR) or first return (FR)	Crown loss		Leaf discolouration		Leaf loss		Browseline		Pong dung		Deer dung		Crown condition		Bulk density	
		r	*p*	*R*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
Max.Height	FR	-0.174	0.1	-0.256	0.01	-0.31	0	-0.08	0.42	-0.26	0.01	0.146	0.156	-0.253	0.01	-0.179	0.08
Ave.Height	FR	-0.022	0.84	-0.104	0.31	-0.04	0.68	-0.07	0.49	-0.27	0.01	-0.17	0.091	-0.115	0.27	0.008	0.94
SD.Height	FR	-0.15	0.16	-0.064	0.54	-0.11	0.29	-0.02	0.84	**0.29**	0.005	0.203	0.047	0.058	0.57	0.155	0.13
H95	FR	-0.141	0.19	-0.138	0.18	-0.17	0.09	-0.24	0.02	-0.12	0.241	-0.04	0.709	-0.134	0.19	-0.083	0.42
H50	FR	0.027	0.8	-0.117	0.26	0.003	0.98	-0.05	0.61	-0.27	0.009	-0.14	0.188	-0.029	0.78	0.007	0.95
Canopy.perm	FR	0.126	0.24	-0.085	0.41	0.138	0.18	-0.28	0.01	-0.11	0.302	-0.16	0.125	0.147	0.15	-0.102	0.32
Can.Closure	FR	-0.105	0.33	-0.241	0.02	-0.15	0.15	-0.08	0.44	-0.17	0.105	-0.13	0.222	-0.207	0.04	0.032	0.75
Ground	FR	0.093	0.39	0.241	0.02	0.144	0.16	0.081	0.43	0.158	0.127	0.127	0.217	0.188	0.07	-0.023	0.82
Understorey	FR	-0.174	0.11	-0.247	0.02	-0.23	0.03	-0.05	0.61	**0.32**	0.001	**0.38**	<0.001	-0.183	0.08	-0.034	0.74
Overstorey	FR	-0.053	0.62	-0.156	0.13	-0.08	0.44	-0.06	0.57	-0.22	0.034	-0.19	0.059	-0.141	0.17	0.036	0.73
VDR	FR	-0.03	0.79	0.13	0.21	-0.01	0.93	0.041	0.69	0.254	0.013	0.128	0.213	0.029	0.78	-0.028	0.78
Max.Height	AR	-0.174	0.1	-0.256	0.01	-0.31	0	-0.08	0.42	-0.26	0.01	0.146	0.156	-0.253	0.01	-0.179	0.08
Ave.Height	AR	-0.005	0.96	-0.114	0.27	-0.04	0.74	-0.1	0.36	-0.24	0.021	-0.2	0.056	-0.093	0.37	-0.008	0.94
SD.Height	AR	-0.109	0.31	-0.067	0.52	-0.08	0.45	-0.13	0.22	0.186	0.072	0.15	0.145	0.086	0.4	0.15	0.14
H95	AR	-0.122	0.26	-0.108	0.29	-0.14	0.17	-0.23	0.02	-0.11	0.308	-0.04	0.695	-0.106	0.31	-0.051	0.62
H50	AR	0.007	0.95	-0.133	0.2	-0.03	0.78	-0.04	0.73	-0.24	0.019	-0.12	0.234	-0.075	0.47	0.03	0.77
Canopy.perm	AR	0.114	0.29	-0.113	0.27	0.115	0.26	-0.28	0.01	-0.09	0.416	-0.16	0.13	0.127	0.22	-0.093	0.37
Can.Closure	AR	-0.154	0.15	-0.272	0.01	-0.2	0.06	-0.06	0.55	-0.15	0.164	-0.12	0.231	-0.262	0.01	0.036	0.73
Ground	AR	0.144	0.18	0.273	0.01	0.193	0.06	0.062	0.55	0.134	0.199	0.125	0.224	0.243	0.02	-0.027	0.8
Understorey	AR	-0.165	0.13	-0.246	0.02	-0.2	0.05	-0.02	0.87	0.283	0.006	**0.39**	**<0.001**	-0.172	0.09	-0.03	0.77
Overstorey	AR	-0.1	0.36	-0.185	0.07	-0.13	0.22	-0.05	0.62	-0.19	0.064	-0.2	0.054	-0.193	0.06	0.038	0.71
VDR	AR	-0.01	0.93	0.146	0.16	0.023	0.82	0.023	0.83	0.231	0.025	0.119	0.247	0.077	0.46	-0.049	0.64

4.4.2. Biodiversity and lidar-derived relationships

Of all the biodiversity data, ground flora richness showed the most common relationships with lidar-derived data (Fig. 4.2; Tables 4.7 – 4.9; Tables A4.31- Table A4.33), which fit the selection criteria of the top model i) including a linear or non-linear relationship, ii) having $\Delta AIC > 4$ from the null model and iii) $r^2 > 0.4$. Ground flora richness mostly had r^2 values ranging from 0.62 – 0.70 when both transects results were combined. There was one exception; SD height had no relationship with ground flora in the AR analysis. In the fenced transect only, four of the lidar-derived variables showed substantial relationships with ground flora for the FR data and six for the AR data (r^2 range = 0.42 – 0.45 for both). For the unfenced data, ECM richness and seedling abundance had two substantial relationships each for the FR data, while there were one and two respectively for the AR data. For ECM, the percentage of returns in the ground layer was considered a substantial relationship for both AR and FR (R^2 range = 0.45 – 0.51), while canopy closure also was included for the AR data (r^2 = 0.4). The maximum height and the understorey were the two substantial relationships for seedling abundance in the unfenced transect (r^2 range = 0.44 – 0.63). For ground flora richness in the unfenced plot, the most parsimonious models were all null models.

4.4.3. Structural stand condition and lidar-derived relationships

The tree condition field measurements came from only the fenced transect. Of the tree condition metrics, leaf discoloration and leaf loss exhibited the most substantial relationships with lidar-derived data using the selection criteria of this study (Fig 4.3). Leaf discoloration, canopy closure, canopy permeability and percentage of returns in the overstorey layer were substantial relationships for both AR and FR data, all of which were non-linear relationships (r^2 range = 0.40 – 0.88). Leaf loss showed three substantial relationships to lidar-derived variables for both AR and FR (r^2 range = 0.52 – 0.92, range ΔAIC = 27.40 – 50.80): average height, canopy closure and overstorey, with a fourth for AR alone: canopy permeability (r^2 = 0.42, ΔAIC = 34.99). Canopy closure and overstorey also showed substantial non-linear relationships with structural crown loss for FR and AR (r^2 range = 0.51 – 0.92, ΔAIC range = 26.03 – 43.05) plus canopy permeability for just AR (r^2 = 0.61, ΔAIC = 34.52). In general, higher r^2 values were present for tree condition relationship when analysing the AR data. Crown condition never displayed any substantial relationships with the lidar-derived measures used in this study (Table 4.7; Table A4.31).

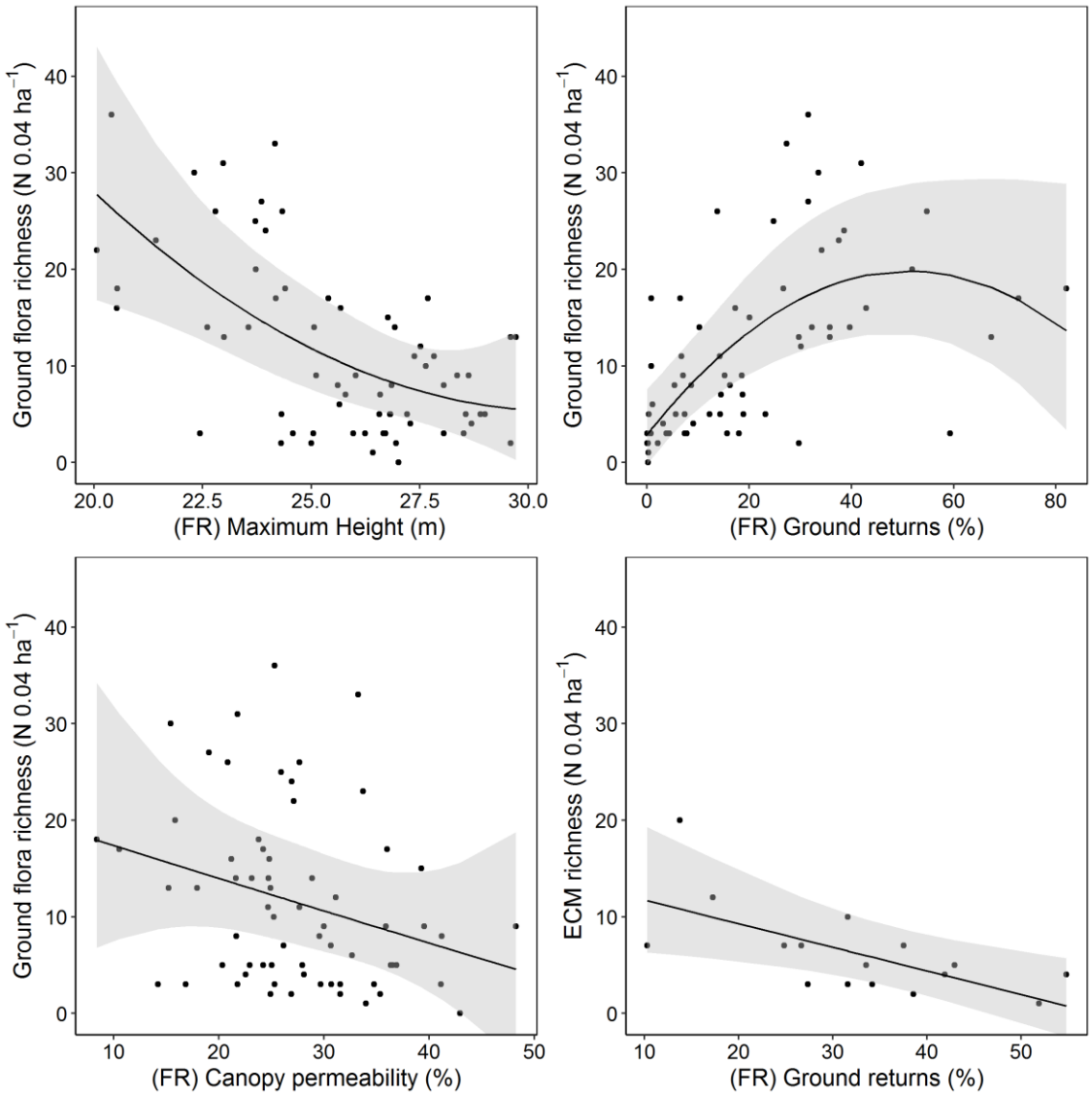

Fig. 4.2. Relationships between lidar-derived variables and biodiversity measures. Solid black lines represent predictions from the most parsimonious GLMs, with grey areas representing 95% confidence intervals of the predictions. AR and FR indicate that the lidar data used were all returns or first returns only, respectively.

4.4.4. Soil content and lidar-derived structure relationships

The carbon and nitrogen soil content and the C:N ratio only displayed weak relationships (r^2 range = 0.07 – 0.21); therefore, none of these were considered substantial based on the criteria of this study. The distribution of different soil elements had some relationships with the lidar variables. These were most pronounced in the unfenced transect with the percentage of silt (2-63 µm sized particles) exhibiting substantial non-linear relationships with canopy closure (Fig 4.3), ground, and maximum height (Fig 4.3) for FR data (r^2 range = 0.41 – 0.55, ΔAIC range = 5.25 – 15.22). The relationship between silt and maximum height was a downward-facing concave relationship, with lower silt

percentages relating to lower maximum heights. Silt and canopy close was represented by an upward-facing concave relationship, where highest recorded percentages of silt related to the least canopy closure. However, the confidence intervals for silt are quite large. For both the AR and FR data used, the percentage of clay (0-2 µm sized particles) only had a single substantial relationship, a non-linear trend with SD height (r^2 = 0.49/0.56, ΔAIC = 12.63/19.64 (FR/AR)). Neither bulk density nor any of the herbivore metrics showed any substantial relationships with the lidar-derived metrics (Tables 4.7 – 4.9; Tables A4.31- A4.33).

One consistent finding of this study was that of outliers, data points that could not be 'normalised' regardless of the transformation used. This was especially prominent in the cases of individual tree condition assessment, which largely related to trees that were either dead but still upright or ones that had lost their crowns but were still living. There were a few examples of this occurrence within the transects in this study, which can clearly be seen in Fig 4.3, where data points in the top-left of each graph represent plots that had the standing but crownless trees. Outliers were also sometimes present in the best fitting models for biodiversity, mainly for seedling abundance, but occasionally for ECM and ground flora.

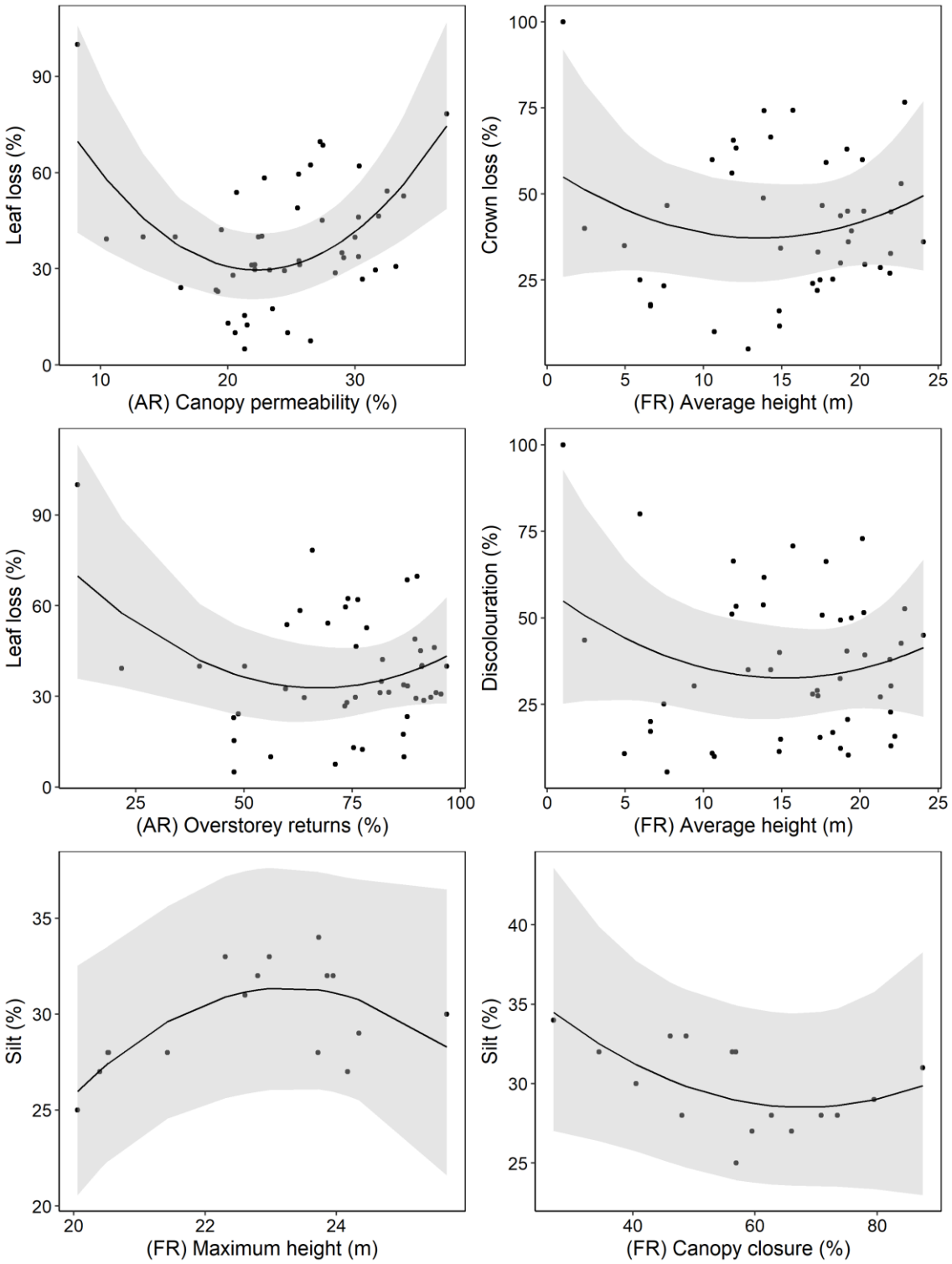

Fig. 4.3. Relationships between lidar-derived variables and individual stand condition measures. Solid black lines represent predictions from the most parsimonious GLMs, with grey areas representing 95% confidence intervals of the predictions. AR and FR indicate that the lidar data used were all returns or first returns only, respectively.

Table 4.7a: Most parsimonious generalised linear models of field-collected condition measures for both transects from 2014 against lidar-derived first returns (FR) metrics from 2010 lidar point cloud data. Values shown in bold are considered substantial relationships based on fitting the criteria of ΔAIC > 4 from the null model and if the $r^2 > 0.4$. Null indicates that the null model was the most parsimonious. See Table 4.3. for lidar metric abbreviations.

Both transects		**Lidar metrics (FR)**										
Field data		AH	CC	CP	Gr	H50	H95	MH	Over	SDH	Under	VDR
Ground flora richness	Model	**Linear**	**Non-linear**	**Non-linear**	**Non-linear**	**Non-linear**	**Non-linear**	**Non-linear**	**Non-linear**	**Non-linear**	**Non-linear**	**Non-linear**
	r^2	**0.7**	**0.691**	**0.622**	**0.683**	**0.681**	**0.652**	**0.654**	**0.69**	**0.652**	**0.691**	**0.694**
	ΔAIC	**105.77**	**88.8**	**8.74**	**76.9**	**79.59**	**45.49**	**35**	**92.01**	**40.03**	**92.3**	**92.3**
ECM richness	Model	Non-linear	Non-linear	Non-linear	Non-linear	Non-linear	Null	Null	Non-linear	Non-linear	Non-linear	Non-linear
	r^2	0.094	0.152	0.086	0.101	0.123	-	-	0.134	0.095	0.061	0.111
	ΔAIC	16.94	47.31	9.84	23.11	30.31	-	-	38.83	14.31	2.77	26.18
Seedling richness	Model	Non-linear	Non-linear	Non-linear	Linear	Non-linear	Non-linear	Linear	Non-linear	Non-linear	Non-linear	Linear
	r^2	0.321	0.294	0.154	0.334	0.254	0.298	0.234	0.267	0.156	0.142	0.291
	ΔAIC	66.33	55.94	15.29	69.42	49.49	56.53	1	49.63	15.24	13.55	58.2
Seedlings abundance	Model	Non-linear	Non-linear	Linear	Non-linear	Non-linear	Linear	Null	Non-linear	Linear	Non-linear	Non-linear
	r^2	0.272	0.32	0.243	0.273	0.256	0.192	-	0.271	0.226	0.259	0.274
	ΔAIC	52.36	75.37	37.41	55.32	38.18	3.26	-	53.02	19.3	40.42	52.42
Soil N	Model	Linear	Linear	Non-linear	Linear	Linear	Linear	Linear	Linear	Non-linear	Non-linear	Linear
	r^2	0.06	0.041	0.011	0.032	0.071	0.122	0.115	0.051	0.081	0.07	0.061
	ΔAIC	24.48	17.4	4.81	12.84	31.35	52.48	46.46	24.35	34.55	29.72	26.11
Soil C	Model	Linear	Linear	Non-linear	Linear	Non-linear	Linear	Linear	Linear	Non-linear	Non-linear	Non-linear
	r^2	0.121	0.114	0.064	0.082	0.122	0.124	0.092	0.123	0.042	0.091	0.113
	ΔAIC	56.09	50.04	26.71	41.28	52.96	51.7	39.45	56.79	16.17	41.99	48.01

Table 4.7b: Most parsimonious generalised linear models of field-collected condition measures for both transects from 2014 against lidar-derived first returns (FR) metrics from 2010 lidar point cloud data. Values shown in bold are considered substantial relationships based on fitting the criteria of ΔAIC > 4 from the null model and if the $r^2 > 0.4$. Null indicates that the null model was the most parsimonious. See Table 4.3. for lidar metric abbreviations.

Both transects		**Lidar metrics (FR)**										
Field data		AH	CC	CP	Gr	H50	H95	MH	Over	SDH	Under	VDR
CN Ratio	Model	Linear	Non-linear	Linear	Linear	Linear	Null	Non-linear	Non-linear	Non-linear	Non-linear	Non-linear
	r^2	0.03	0.04	0.07	0.04	0.01	-	<0.01	0.04	0.08	0.02	0.03
	ΔAIC	15.42	23.27	33.05	24.78	5.11	-	1.93	20.76	43.87	7.48	12.44
Clay	Model	Linear	Non-linear	Linear	Non-linear	Non-linear	Non-linear	Linear	Non-linear	Non-linear	Non-linear	Non-linear
	r^2	0.16	0.24	0.11	0.07	0.1	0.04	0.02	0.22	0.2	0.06	0.09
	ΔAIC	35.41	49.24	16.14	18.4	14.37	8.11	1.09	44.27	59.03	10.91	15.8
Silt	Model	Non-linear	Non-linear	Linear	Non-linear	Linear	Linear	**Non-linear**	Non-linear	Linear	Linear	Non-linear
	r^2	0.24	0.25	0.03	0.24	0.17	0.16	**0.43**	0.24	0.07	0.08	0.15
	ΔAIC	69.02	67.12	0.69	63.07	47.14	58.55	**6.09**	61.42	7.06	20.75	2
Sand	Model	Non-linear	Non-linear	Linear	Non-linear	Linear	Linear	Non-linear	Non-linear	Non-linear	Non-linear	Non-linear
	r^2	0.21	0.3	0.08	0.08	0.15	0.09	0.07	0.28	0.16	0.08	0.14
	ΔAIC	98.23	153.54	35.09	32.59	66.76	41.42	27.35	136.97	77.64	29.6	2
Bulk density	Model	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null
	r^2	-	-	-	-	-	-	-	-	-	-	-
	ΔAIC	-	-	-	-	-	-	-	-	-	-	-

Table 4.8a: Most parsimonious generalised linear models of field-collected condition measures for the fenced transect from 2014 against lidar-derived first returns (FR) metrics from 2010 lidar point cloud data. Values shown in bold are considered substantial relationships based on fitting the criteria of ΔAIC > 4 from the null model and if the $r^2 > 0.4$. Null indicates that the null model was the most parsimonious. See Table 4.3. for lidar metric abbreviations.

Fenced transect		**Lidar metrics (FR)**										
Field data		AH	CC	CP	Gr	H50	H95	MH	Over	SDH	Under	VDR
Ground flora richness	Model	**Linear**	**Linear**	Null	**Linear**	Linear	Null	Null	**Linear**	Linear	Null	Linear
	r^2	**0.45**	**0.44**	-	**0.44**	0.41	-	-	**0.44**	0.38	-	0.42
	ΔAIC	**6.57**	**5.72**	-	**6.08**	3.23	-	-	**5.89**	1.56	-	3.83
ECM richness	Model	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null
	r^2	-	-	-	-	-	-	-	-	-	-	-
	ΔAIC	-	-	-	-	-	-	-	-	-	-	-
Seedling richness	Model	Linear	Linear	Non-linear	Linear	Linear	Linear	Linear	Linear	Null	Null	Linear
	r^2	0.29	0.3	0.16	0.27	0.23	0.17	0.16	0.27	-	-	0.22
	ΔAIC	6.7	7.11	2.04	6.25	4.75	2.43	2.66	6.21	-	-	4.7
Seedlings abundance	Model	Non-linear	Non-linear	Linear	Non-linear	Non-linear	Non-linear	Null	Non-linear	Linear	Linear	Non-linear
	r^2	0.32	0.3	0.18	0.3	0.25	0.29	-	0.31	0.19	0.22	0.28
	ΔAIC	8.24	8.57	2.29	8.5	3.28	56.53	-	7.57	2.43	3.47	6.02
Soil N	Model	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null
	r^2	-	-	-	-	-	-	-	-	-	-	-
	ΔAIC	-	-	-	-	-	-	-	-	-	-	-
Soil C	Model	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null
	r^2	-	-	-	-	-	-	-	-	-	-	-
	ΔAIC	-	-	-	-	-	-	-	-	-	-	-

Table 4.8b: Most parsimonious generalised linear models of field-collected condition measures for the fenced transect from 2014 against lidar-derived first returns (FR) metrics from 2010 lidar point cloud data. Values shown in bold are considered substantial relationships based on fitting the criteria of ΔAIC > 4 from the null model and if the r^2 > 0.4. Null indicates that the null model was the most parsimonious. See Table 4.3. for lidar metric abbreviations.

Fenced transect		Lidar metrics (FR)										
Field data		AH	CC	CP	Gr	H50	H95	MH	Over	SDH	Under	VDR
CN Ratio	Model	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null
	r^2	-	-	-	-	-	-	-	-	-	-	-
	ΔAIC	-	-	-	-	-	-	-	-	-	-	-
Clay	Model	Linear	Linear	Linear	Linear	Null	Null	Null	Linear	**Non-linear**	Null	Null
	r^2	0.33	0.34	0.33	0.33	-	-	-	0.34	**0.49**	-	-
	ΔAIC	2.31	4.07	2.38	2.46	-	-	-	3.42	**12.63**	-	-
Silt	Model	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null
	r^2	-	-	-	-	-	-	-	-	-	-	-
	ΔAIC	-	-	-	-	-	-	-	-	-	-	-
Sand	Model	Linear	Non-linear	Null	Non-linear	Null	Null	Null	Non-linear	Non-linear	Non-linear	Null
	r^2	0.12	0.19	-	0.17	-	-	-	0.28	0.28	0.08	-
	ΔAIC	3.3	5.52	-	3.63	-	-	-	136.97	11.67	29.6	-
Leaf discolouration	Model	Null	**Non-linear**	**Non-linear**	Non-linear	Non-linear	Null	Linear	**Non-linear**	Null	Null	Non-linear
	r^2	-	**0.58**	**0.4**	0.21	0.28	-	0.17	**0.54**	-	-	0.17
	ΔAIC	-	**35.29**	**26.32**	4.1	13.55	-	2.85	**28.7**	-	-	1.67
Leaf loss	Model	**Non-linear**	**Non-linear**	Non-linear	Non-linear	Non-linear	Linear	Linear	**Non-linear**	Null	Null	Null
	r^2	**0.53**	**0.92**	0.34	0.21	0.19	0.09	0.07	**0.52**	-	-	-
	ΔAIC	**27.4**	**49.49**	28.56	4.1	11.87	8.27	6.67	**30.44**	-	-	-

Table 4.8c: Most parsimonious generalised linear models of field-collected condition measures for the fenced transect from 2014 against lidar-derived first returns (FR) metrics from 2010 lidar point cloud data. Values shown in bold are considered substantial relationships based on fitting the criteria of ΔAIC > 4 from the null model and if the $r^2 > 0.4$. Null indicates that the null model was the most parsimonious. See Table 4.3. for lidar metric abbreviations.

Fenced transect		**Lidar metrics (FR)**										
Field data		AH	CC	CP	Gr	H50	H95	MH	Over	SDH	Under	VDR
Structural crown loss	Model	**Non-linear**	**Non-linear**	Non-linear	Null	Non-linear	Linear	Linear	**Non-linear**	Linear	Non-linear	Null
	r^2	**0.93**	**0.91**	0.32	-	0.19	0.08	0.05	**0.51**	0.02	0.06	-
	ΔAIC	**43.68**	**42.13**	19.36	-	10.12	6.38	2.51	**26.03**	2.16	3.07	-
Browseline	Model	Null	Null	Linear	Null	Null	Null	Null	Null	Linear	Null	Null
	r^2	-	-	0.11	-	-	-	-	-	<0.01	-	-
	ΔAIC	-	-	1.66	-	-	-	-	-	1.94	-	-
Crown condition	Model	Null	Null	Non-linear	Null	Null	Null	Linear	Null	Null	Non-linear	Null
	r^2	-	-	0.13	-	-	-	0.04	-	-	0.08	-
	ΔAIC	-	-	5.47	-	-	-	1.85	-	-	1.86	-
Bulk density	Model	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null
	r^2	-	-	-	-	-	-	-	-	-	-	-
	ΔAIC	-	-	-	-	-	-	-	-	-	-	-
Pony dung	Model	Null	Non-linear	Null	Non-linear	Non-linear	Null	Null	Null	Null	Linear	Non-linear
	r^2	-	0.08	-	0.08	0.12	-	-	-	-	0.06	0.1
	ΔAIC	-	2.99	-	3.13	6.12	-	-	-	-	2.64	3.13
Deer dung	Model	Null	Null	Null	Null	Null	Null	Null	Null	Null	Linear	Null
	r^2	-	-	-	-	-	-	-	-	-	0.211	-
	ΔAIC	-	-	-	-	-	-	-	-	-	2.97	-

Table 4.9a: Most parsimonious generalised linear models of field-collected condition measures for the unfenced transect from 2014 against lidar-derived first returns (FR) metrics from 2010 lidar point cloud data. Values shown in bold are considered substantial relationships based on fitting the criteria of ΔAIC > 4 from the null model and if the $r^2 > 0.4$. Null indicates that the null model was the most parsimonious. See Table 4.3. for lidar metric abbreviations.

Unfenced transect		**Lidar metrics (FR)**										
Field data		AH	CC	CP	Ground	H50	H95	MH	Over	SDH	Under	VDR
Ground flora richness	Model	Null	Non-linear	Linear	Null	Null	Null	Null	Null	Non-linear	Non-linear	Non-linear
	r^2	-	0.5	0.44	-	-	-	-	-	0.51	0.49	0.5
	ΔAIC	-	3	1.9	-	-	-	-	-	3.51	2.02	3.18
ECM richness	Model	Null	**Linear**	Null	**Linear**	Linear	Null	Null	Null	Null	Null	Non-linear
	r^2	-	**0.4**	-	**0.51**	0.18	-	-	-	-	-	0.55
	ΔAIC	-	**13.54**	-	**19**	3.91	-	-	-	-	-	2.75
Seedling richness	Model	Null	Null	Null	Null	Null	Null	Null	Null	Null	Non-linear	Null
	r^2	-	-	-	-	-	-	-	-	-	0.57	-
	ΔAIC	-	-	-	-	-	-	-	-	-	2.06	-
Seedlings abundance	Model	Null	Null	Null	Null	Null	Linear	**Non-linear**	Null	Linear	**Non-linear**	Null
	r^2	-	-	-	-	-	0.259	**0.445**	-	0.259	**0.55**	-
	ΔAIC	-	-	-	-	-	32.606	**39.14**	-	31.955	**64.03**	-
Soil N	Model	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null
	r^2	-	-	-	-	-	-	-	-	-	-	-
	ΔAIC	-	-	-	-	-	-	-	-	-	-	-
Soil C	Model	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null
	r^2	-	-	-	-	-	-	-	-	-	-	-
	ΔAIC	-	-	-	-	-	-	-	-	-	-	-

Table 4.9b: Most parsimonious generalised linear models of field-collected condition measures for the unfenced transect from 2014 against lidar-derived first returns (FR) metrics from 2010 lidar point cloud data. Values shown in bold are considered substantial relationships based on fitting the criteria of ΔAIC > 4 from the null model and if the r^2 > 0.4. Null indicates that the null model was the most parsimonious. See Table 4.3. for lidar metric abbreviations.

Unfenced transect		**Lidar metrics (FR)**										
Field data		AH	CC	CP	Ground	H50	H95	MH	Over	SDH	Under	VDR
CN.Ratio	Model	Null	Null	Null	Null	Null	Non-linear	Non-linear	Null	Non-linear	Null	Null
	r^2	-	-	-	-	-	0.29	0.36	-	0.18	-	-
	ΔAIC	-	-	-	-	-	5.77	9.13	-	1.01	-	-
Clay	Model	Non-linear	Linear	Null	Non-linear	Non-linear	Null	**Non-linear**	Linear	Null	Null	Non-linear
	r^2	0.22	0.17	-	0.38	0.25	-	**0.52**	0.3	-	-	0.25
	ΔAIC	2.93	3.35	-	10.23	4.22	-	**18.48**	8.07	-	-	4.05
Silt	Model	Non-linear	**Non-linear**	**Linear**	**Non-linear**	Null	Null	**Non-linear**	Non-linear	Null	Linear	Null
	r^2	0.246	**0.41**	**0.53**	**0.42**	-	-	**0.55**	0.44	-	0.28	-
	ΔAIC	6.092	**5.25**	**15.22**	**7.21**	-	-	**13.75**	6.67	-	2.77	-
Sand	Model	Non-linear	Non-linear	Null	**Non-linear**	Non-linear	Null	Null	Linear	Null	Null	**Non-linear**
	r^2	0.34	0.32	-	**0.43**	0.39	-	-	0.24	-	-	**0.41**
	ΔAIC	8.39	7.11	-	**13.4**	10.33	-	-	6.63	-	-	**11.37**

4.5. Discussion

The main results of this study show that some lidar-derived measures could potentially be used to infer ecological woodland condition values, the consequences of which would provide a vital tool to help quantify forest condition with limited resources (Aplin, 2005; Hill et al. 2014). For example, relating specifically to forest biodiversity, ground flora richness was the metric that could best be inferred through the use of lidar-derived metrics. In fact, most of the lidar metrics used in this study exhibited a substantial relationship with ground flora richness (r^2 = 0.62 – 0.70), with the exception of the standard deviation of the height in the AR data. Similarly, the results suggest that lidar has a usefulness when inferring accurate stand conditions, with two of the best proxy lidar-derived measures for structural crown loss, leaf loss and discolouration being canopy closure and percentage of returns in the overstorey layer (i.e. < 5 m) (r^2 = 0.54 – 0.92). In contrast, the condition of the woodland soil, measured using its carbon and nitrogen content, could not be predicted with lidar variables and therefore could not be inferred through using lidar, at a 0.04 ha scale.

The substantial relationships between ground flora richness and lidar-derived structural metrics agree with the findings of other research, which suggest that forest flora diversity can be predicted by lidar (Simonson et al. 2012; Wolf et al. 2012). Canopy height specifically, which exhibited strong relationships to ground flora richness (r^2 = 0.65 – 0.70) in this study, has also been shown to be a good predictor of ground flora species richness in tropical and temperate, mountainous forests (Wolf et al. 2012; Lopatin et al. 2016). Interestingly however, while in this study canopy closure and canopy permeability were strongly related to ground flora species richness (r^2 = 0.62 – 0.69), a Mediterranean temperate forest study (Lopatin et al. 2016) showed that the canopy structural properties (canopy contrast and canopy dissimilarity) are seen to be of little importance when prediciting floral richness. The differences could be due to the dissimilarities in the life histories of the dominant species present. For example, *Cryptocarya alba*, one of the dominant species in Lopatin et al. (2016), inhabits south-facing slopes (Armesto and Martinez, 1978) where light is less of a limiting factor to ground flora, whereas the dominant species in this study, beech (*Fagus sylvatica*), creates almost entirely closed canopies in the summer, making light a very limiting factor for understorey vegetation (Brown, 1953; Peters, 1997; Gálhidy et al. 2006).

The relatedness of ground flora to most lidar-derived variables provides evidence for the hypothesis that lidar could be used to infer measures of ecological habitat condition. However, there was little evidence to support this in the other biodiversity

measures recorded (i.e. ECM, seedlings richness and seedling abundance). In this study, strong relationships were only exhibited between lidar metrics and ECM species richness in the unfenced transect and then only for one metric when using both FR and AR data, namely the percentage of returns that come from the ground layer. These findings are in contrast to previous research by Peura et al. (2016), which showed that lidar-derived average diameter at breast height and deciduous tree volume are good predictors of fungi abundance, although ECM richness, which was measured in this study, was not measured, and Gómez-Hernández et al. (2012), who found that canopy openness and tree density were important in ECM richness. The reason the results here did not show relationships between ECM richness and lidar-derived variables may be due to the time delay between the lidar and field study. Although suitable light and nutrient regimes can sustain early successional ground flora communities for years, especially when high herbivory pressure helps to alleviate competition of some of the faster growing plants (Kirby, 2001), ECM reduction can follow tree damage within a single season (Saravesi et al. 2008). Temporal analysis of simultaneous lidar and field assessments may therefore be needed to better determine if lidar metrics can be used to detect woodland ECM condition.

Evidence for the hypothesis that lidar-derived variables could be used to infer stand condition was presented in the results of this study, as strong relationships existed between lidar-derived canopy closure and overstorey returns and the individual conditions of the crowns, namely the percentage of leaf loss, structural crown loss and discolouration. This is perhaps unsurprising as the main purpose of lidar use is to map structure (Jones and Vaughan, 2010). However, since there was a four-year difference between lidar acquisition and field data collection, different inferences could be made. First, is that over those four years, the forest structure did not change much. This is likely, due to large declines in woodland basal area of Denny Wood being more attributed to drought conditions (Tubbs, 2001; Mountford and Peterken, 2003; Martin et al. 2015), conditions that have not been as prevalent in recent years as previously (Cavin and Jump, 2017). This is supported by Martin et al. (*in press*) in a study which showed an overall positive trend in basal area over the last 15 years in Denny Wood. Another inference that could be made is that lidar metrics could be used as predictions for forest condition in the future based on processes occurring at that time. This phenomenon is shown in a study by Coops et al. (2009), in which comparisons between lidar returns from coniferous trees that had been attacked by beetles in the past and those that had not gave significantly different results. This infers that lidar-derived health metrics (which could potentially include leaf loss, discolouration and crown structural loss) could be used to determine

which trees/ stands have been impacted by a threat/ stressor. In Denny Wood, trees could be inflicted by drought stress (Martin et al. 2015) or by pathogens, which are increasingly impacting European temperate species (Santini et al. 2013), both of which may contribute to the strong relationships observed in this study.

Field-collected soil condition and lidar-derived metrics were often significantly correlated. From the correlation results, the clay, silt and sand content of the soil all highly correlated with both overstorey development and canopy closure, with clay and silt correlating negatively with both lidar variables and sand content correlating positively. The implication of these highly significant correlations is that the soil structure may have been a driving influence for the development of the overstorey layer and the canopy stucture which affects the growing condition of the understorey and ground vegetation. Therefore, the soil structure may be a major factor in determining whether beech is likely to undergo severe dieback or not. However, the results of this Chapter were in contrast to the findings of Martin et al. (2017), a study which found that the soil clay content did not affect tree mortality in Denny Wood. While more studies need to be conducted, especially in other locations, the correlation results from this Chapter indicate that the use of lidar may have application in being able to explain beech decline, even if it cannot be fully utilised to monitor ongoing dieback and thus resilience. Thus, this indicates that the condition of the soil may have historically affected the structure of the stand, and therefore the lidar variables, rather than the other way around. While this notion needs to be fully tested, it is conceivable due to the important role that fertility of soil plays in the health of woodland stands during stand development through chemical, structural and biological pathways (Ponette et al. 2014; Crann et al. 2015). Hartmann et al. (2012) showed how historic disturbance in coniferous forests affected the microbial composition in the long-term, and Avila et al. (2016) determined that historic dieback caused reductions in soil respiration and nutrient cycling. In future lidar work, to see if remote sensing could be used to determine more dynamic soil condition, analysis could pertain to tree leaf mineral analysis or biological soil analysis, which both change more dynamically that nutrients in soil (Hartmann et al. 2012; Ponette et al. 2014; Crann et al. 2015), although other factors such as stand age would also need to be considered in that instance (Duquesnay et al. 2000).

The occurrence of outliers in this study could be a potential limitation of using lidar for the purpose of inferring woodland condition, especially individual tree condition, based on the results here. The challenge in including snags (i.e. the cause of outliers) in the lidar assessment of old growth forest is acknowledged, especially as the structure is

different to living, leaved trees (Bater et al. 2009). This challenge is also likely to be accentuated in studies of dying old growth forest, where the density of standing dead wood stems can range from 12 to 79 per hectare, on average (McGee et al. 1999). To overcome this issue, the use of spectral data in conjunction with lidar could confirm trees that are dead, as spectral indices such as the Normalized Differenced Vegetation Index are relatively good complementary indicators for ecological lidar data collection (Swatantran et al. 2011). In addition, techniques such as robust regression have been used to limit the effect of outliers when using lidar and field collected data together (Morsdorf et al. 2004). However, the main assumption of that technique is that most of the data points form a linear relationship, which was not the case here.

Another limitation on the scope of this study is the time difference between lidar acquisition and field data collection, which were approximately four years apart. Looking at the change of forest bird species richness with a six-year time gap between lidar and field data collection, Vierling et al. (2014) found that there was little temporal change. However, that was for a single ecosystem and for a mobile animal group. For this study, especially as the study site has historically undergone dieback, both tree conditions and change in species richness of less mobile biodiversity (e.g. ECM) could have changed varying amounts within the 4-year period. Furthermore, lidar ignores the drivers of what may be causing any changes and the history of the forest, an often-forgotten consideration (Hermy and Verheyen, 2007). Therefore to apply the findings here to other locations, such factors would have to be accounted for and considered, together with structure and frequency of field-data collection (Lopatin et al. 2016).

4.6. Conclusions and usefulness for inferring resilience

The results presented here provide evidence for the hypotheses that lidar can be used to infer biodiversity and stand condition of a forest stand, thereby illustrating that lidar has some utility for inferring the condition of other properties of the forest. However, biodiversity and lidar-derived metric relationships mainly pertained to ground flora, and not important functional forest components such as ECM. Moreover, the results also lack evidence with regards to being able to infer the condition of driving influences (herbivory in this study), and important factors such as soil condition. These findings emphasise the challenges that arise through using lidar as the only source of data, especially if trying to infer what the future condition of the particular forest might be.

In Chapter 2, it was discovered that ground flora changed relatively to declining woodland condition, based on the most parsimonious model. This is therefore a slow-

changing variable, which is needed as the basis for resilience assessments (Carpenter et al. 2001; Bennett et al. 2005). Consequently, it could be determined that lidar metrics could be used as surrogate resilience assessments measures, as certain lidar-derived measures could predict ground flora richness in this study. However, the relationships between ground flora and lidar metrics were mostly non-linear. This means that different values of a lidar variable could give the same value of species richness, making them unsuitable for resilience assessments. Moreover, ECM richness changed gradually after the first stage of dieback in Chapter 2, demonstrating an opposite trend to ground flora richness. Thus, it would be expected that ECM would show an opposite trend to lidar variables than ground flora richness did, but ECM only related to lidar metrics in a single transect in this study. In this way, lidar variables could not be used as accurate surrogates in resilience assessments. Nonetheless, this may change if the study was repeated with no time lag between field and lidar measurements.

Chapter 5:
The effect of woodland cover on the resilience of a temperate ecosystem

5.1. Abstract

Current landscape-scale management approaches aim to increase resilience over the landscape through increasing connectivity. However, experimental data showing relationships between landscape connectivity and resilience are rare, largely owing to the sizable temporal and spatial scales required for real-life experiments. Therefore, a quantitative forest succession modelling (LANDIS-II) approach was used in this study. The resistance, persistence and recovery time – the three engineering resilience attributes – of 10 important woodland ecosystem properties were assessed in response to a pulse disturbance, across a gradient of initial woodland cover (WC), a commonly-used metric of connectivity. An additional press disturbance was included for half of the simulations, used to simulate herbivory. Specifically, the following hypothesis was tested: initial woodland cover influences landscape resilience under different disturbance intensities. Results showed that WC influenced a majority of the resilient attributes for the individual ecosystem properties. Often, the resilient attributes responded in a non-linear way across the WC gradient, with intermediate WC (50%-75% WC) landscapes frequently having more favourable resilience (i.e. higher resistance and persistence, and a lower recovery time). This was attributed to the non-dominance of a single tree species at the intermediate WC landscapes, whereas 25% and 100% WC landscapes were dominated by a single species. Additionally, the opportunity of natural expansion was curtailed in the 100% WC landscape, impacting persistence and recovery. Lastly, herbivory had a marked, mostly negative, effect on the persistence and recovery time of ecosystem properties.

5.2. Introduction

Woodland threats and stressors including large-scale deforestation, habitat fragmentation of woodland, climate change and land-use change are increasing globally (MEA, 2005; NEA, 2011; Hansen et al. 2013; Allen et al. 2015). Such threats are making the future trends of woodland derived-ecosystem properties uncertain (Park et al. 2014; Trumbore et al. 2015). One of the major detrimental effects currently being recorded is biodiversity loss in terms of species richness, abundance and genetic variation (Fahrig, 2013; Melo et al. 2013). This is often attributed to reductions in connectivity and/or total area of wooded habitats (e.g. Fahrig, 2013; Herrault et al. 2016). Similarly, the quality and quantity of

ecosystem functions and ecosystem services (ES) provisions are also hypothesised to be impacted further due to land cover area and condition modification of wooded landscapes (MEA, 2005; NEA, 2011). These changes affect people's well-being and local and global economies that depend upon these properties being sustained or improved (Ryan et al. 2016).

To provide protection against the impacts of increasing pressures, environmental strategies now often adopt a landscape scale management approach (Scottish Executive, 2004; Watts et al. 2005; Lawton et al. 2010; Defra, 2011; Wikramanayake et al. 2011), integrating strategies for the sustainability of combinations of ecosystem properties (EPs), properties that include biodiversity, ES and ecosystem functions. For example, sustainable forest landscape management often aims to conserve biodiversity and habitats, increase forest health and ES provisions and maintain timber production simultaneously (Messier et al. 2015; Olson et al. 2017). The landscape approach is seen as especially vital with regards to woodlands, as woodland biodiversity loss is predicted to become much more severe and rapid under climate change (Berry et al. 2002; Heller and Zavaleta, 2009; Royo at el. 2010; Lavorel et al. 2014). As ES are often the products of underlying biodiversity (Balvanera et al. 2006; Cardinale et al. 2012), there is a similar concern for the flow and supply of ES and ecosystem functions at landscape scales (Mitchell et al. 2015). However, it is not clear how different EPs will alter with changing landscapes (Biggs et al. 2012); both positive and negative trends are expected (Mitchell et al. 2015).

As part of the recognition of the importance of landscape management, the role of landscape habitat connectivity (or connectedness), which is broadly defined as the degree to which movement and interactions of genetic material, individuals or resources are facilitated across a landscape (Taylor et al. 1993; Goodwin, 2003; Bodin and Prell, 2011; Rudnick et al. 2012), has become a central focus (Lawton et al. 2010; Mitchell et al. 2015). This has resulted in increased habitat connectivity becoming a prominent aim in international environmental policy (Heller and Zavaleta, 2009; Lawton et al. 2010; JNCC, 2012). For example, it is one of the conditions of achievement of the EU's Green Infrastructure Strategy - part of the EU's European Biodiversity Strategy to meet 2020 targets (European Commission, 2013). Similarly, the UK's national strategies aim to tackle declining ES and biodiversity through increasing connectivity (Watts et al. 2005; Lawton et al. 2010; HM Government, 2011).

A major reason that connectivity is perceived as an essential landscape attribute for both ES and biodiversity is because connected environments are also thought to be

more resilient (MEA, 2005; Lawton et al. 2010; Biggs et al. 2012; Tambosi et al. 2014; Mitchell et al. 2015; Seidensticker, 2015), especially for landscapes where climate change is having a major impact (Ayram et al. 2016). This stems partly from metapopulation theory, as a high degree of connectivity should allow for the reorganisation and renewal of biological communities in space (Folke et al. 2004; Seidensticker, 2015). It is therefore believed that achieving high levels of connectivity is important for determining landscape-level resilience (Millar et al. 2007; IPCC, 2014; Standish et al. 2014; Oliver et al. 2015), hence its common use as an aim in conservation efforts (Rudnick et al. 2012; Leite et al. 2013; Tambosi et al. 2014).

The theory that increased connectivity relates to increased resilience has two main problems, however. First, there is a severe lack of evidence relating the two concepts of connectivity and resilience, especially for terrestrial landscapes. There is evidence that increased connectivity relates positively to resilience in aquatic ecosystems, notably coral reefs (Mumby and Hastings, 2008; Adam et al. 2011; Vergés et al. 2011; Olds et al. 2012), and that connectivity enhances the persistence of some biodiversity (Liira and Paal, 2013; Ayram et al. 2016; Jakobsson et al. 2016). However, there has been very little previous research into the effect of connectivity on overall resilience of important EPs (Bailey, 2007; Mitchell et al. 2013).

The second issue with the theory is that connectivity and resilience are both vague and ambiguous terms (Goodwin, 2003; Standish et al. 2014). Connectivity is difficult to define as it is often based on the specific requirements of individual species or ES (Summerville and Crist, 2001; Fisher et al. 2009; Syrbe and Walz, 2012; Rudnick et al. 2012); the scale assessed (Tambosi et al. 2014); and ecological, economical, and social motivations and goals (Biggs et al. 2012; Hodgson et al. 2015; Nimmo et al. 2015). However, both resilience and connectivity definitions need to be clear (Hodgson et al. 2015; Nimmo et al. 2015) and directly measurable so that they can be used operationally in conservation and management strategies (DeRose and Long, 2010; Tambosi et al. 2014; Hodgson et al. 2015; Nimmo et al. 2015).

The vagueness of resilience is explored in Section 1.3. To make resilience more measurable, the definition of engineering resilience can be used (Holling, 1996a; Peterson et al. 1998). There are two main sections of engineering resilience: resistance and recovery (Hodgson et al. 2015; Newton and Cantarello 2015; Nimmo et al. 2015) (Fig. 1.4). In addition to these, persistence – the similarity of an EP value after a period of ecological time – is also an important feature of the landscape resilience (Grimm and Wissel, 1997). Usefully, engineering resilience measurements also incorporates the

intensity of a disturbance, which is key when assessing resilience (Carpenter at al. 2001; Cole et al. 2014; Nimmo et al. 2015).

The amount of habitat area (i.e. the percentage of habitat over a landscape) is often used as a proxy for connectivity as it is known as a good predictor of many EPs. For example, Flather and Bevers (2002) determined that habitat amount alone explained the most variance (97%) for population abundances when compared to spatial configuration. Furthermore, over half (56%) of studies showed habitat patch size, together with isolation, to be the main determinants of biodiversity richness in a meta-analysis by Prevedello and Vieira (2010). Consequently, habitat area has been included in standardised landscape assessments for ES (Frank et al. 2012) and persistence studies of biodiversity (Flather and Bevers, 2002; Ewers, 2004; Prevedello and Vieira, 2010; Jackson and Fahrig, 2015). Thus, habitat area is considered an appropriate proxy metric of connectivity to use when assessing different types of EPs (Goodwin, 2003; Jackson and Fahrig, 2015).

Given that connectivity is used as a proxy for resilience in many landscape management plans, it is important to understand if connectivity has an influence on landscape resilience as this has implications for the future of a landscape (Mitchell et al. 2013; Allen et al. 2016). Moreover, knowledge regarding the factors that influence landscape resilience needs to be obtained with relative haste as rapid environmental change and other land-use pressures progress (Seidl et al. 2016). Such information also must include spatiotemporal aspects of changing resilience - aspects that are often not accounted for yet provide opportunities to predict resilience when combined with connectivity measures (Standish et al. 2014; Rappaport et al. 2015; Allen et al. 2016). Due to the sizable temporal and spatial scales required, this would be difficult to achieve using real-life experiments. Therefore, to address the important knowledge gap that remains as experimental data showing relationships between landscape connectivity and resilience are rare (Mitchell et al. 2013), a novel quantitative forest succession modelling approach was used in this study: the resilience of 10 important woodland EPs were assessed across a gradient of connectivity in response to different intensities of pulse disturbance, with an addition press disturbance included for half the simulations. Initial landscape woodland cover was used as a proxy of connectivity, and resilience was assessed in the measurable attributes of resistance, persistence and recovery time. Specifically, the following hypothesis was tested: initial woodland cover (WC) influences landscape resilience under different disturbance intensities.

5.3. Materials and methods

5.3.1. Study area

The New Forest Special Area of Conservation (SAC) (longitude: $1^0$17'59'' to $1^0$48'8'' W, Latitude: $50^0$42'19'' to $51^0$0'17'' N) is approximately 29,214 ha in area and is situated wholly within the boundaries of New Forest National Park (Fig. 1.5) in southern England. The mean (± S.D.) annual precipitation is 832 ± 150 mm and mean annual temperature is 10.17 ± 0.64 ºC, based on data between 1957 and 2014. The local climate is temperate oceanic (Met Office, 2015). Twenty-nine percent of the SAC (8,472 ha) is classed as broadleaved deciduous woodland, consisting partly of 9120 Atlantic acidophilous beech forest (*Quercion robori petraeae* or *Ilici-Fagenion*) and by 9130 beech forest (*Asperulo-Fagetum*) SAC communities (JNCC, 2011). The SAC also covers other ecologically important habitats including heath and mire.

5.3.2. Study design

The study was designed to test whether initial woodland cover (WC), a proxy measure of habitat connectivity, influenced the resilience of a landscape in response to different intensities of disturbance. To create an initial WC gradient, five initial WC maps were created, each with broadleaved woodland covering a different amount of the landscape (0, 25%, 50%, 75% and 100%). These maps were based on simulations of forest succession in the New Forest, and grounded by empirical data (Section 5.3.3). To be able to assess resilience in response to different intensities of disturbance, five sets of pulse disturbance intensity (PDI) scenarios were conceived, each involving the removal of different tree species (Section 5.3.6.1). Each pulse disturbance was activated after 20 years of simulated forest succession, with different simulations starting from the different initial WC maps. To assess resilience of the EPs in response to the pulse disturbance, values of each EP were recorded at 15, 20, and 170 years into all the simulations, which meant that resistance and persistence could be calculated. Recovery time was measured as the time when the post-disturbance value of an EP equalled that of the pre-disturbance (Section 5.3.9.1). To determine whether additional press disturbances influenced landscape resilience further, the five sets of PDI scenarios were repeated with the inclusion of an additional press disturbance that also began at 20 years and continued for the duration of the simulations (Section 5.3.6.2).

5.3.3. Initial woodland cover maps

The hypothetical compositions of WC were created based on mature woodland (i.e. tree species > 10 years old) data (Newton et al. 2013), and used as the initial woodland layer for the simulations. The initial WC stages used were 0%, 25%, 50%, 75% and 100% as this allowed for the gradient of initial WC to be produced over which the resilience attributes could be tested. Note: all conifers were excluded from this study, therefore WC values refer to broadleaved trees only.

The New Forest SAC consisted of approximately 36.6% WC, after the conifers had been excluded. To get the required higher starting percentages (50%, 75% and 100% WC), a landscape model, LANDIS-II (described below), was run with the Biomass Succession module (Scheller and Mladenoff, 2004) for 400 years, starting from initial WC percentage (i.e. 36.6%). Mapped outputs of the 400-year simulations, which were represented as 50 x 50 m grid squares, were then used to determine the percentage of WC at each year. Each raster grid square contained the ages of all the species present, therefore if mature trees (age $\geq$ 10) of a species were present in the grid square then that square was counted as a WC square, and the percentage cover worked out thusly. Defining the squares as WC was undertaken using the *reclassify* tool in (ArcGIS 10.1), where a value of 0 was given to those that did not contain any mature trees. WC was 74.11% and 99.91% after 13 and 300 years, respectively. These were the closest values to the required values, and therefore were the ones used. The spatial extent and composition output from those years was used to create new initial community maps and inputs for the appropriate WC needed.

Using the steps described above, 50% WC could not be obtained from the results of a single simulation. This was because the percentages for year 10 (35% WC) and year 11 (64% WC) were not close enough to the desired amount. To solve this, the expansion (which was the difference in WC extent between year 10 and year 11 outputs) was calculated using the *raster calculator* tool. Subsequently, the *SelectRandomByPercent* tool was used on the expansion to randomly select cells that equated to 50% WC when combined with the year 10 outputs. To work out the initial communities for the 50% inputs, the year 11 outputs were confined to that of the new layer, and the values of the year 11 cohorts were used. For 25% WC, a landscape map of the New Forest was used that only included non-managed broadleaved woodland. Excluding all other areas and types of woodland, the combined total area of non-managed broadleaved woodland was 24.8% of the whole landscape; therefore it was utilised in this study. For a more detailed explanation of the creation 25% WC map, see Cantarello et al. (*in press*).

For 0% WC, the only species in the initial community were heath species, namely ling heather (C*alluna vulgaris)* and European gorse (*Ulex europaeus*), neither of which are considered timber species. Therefore, the landscape consisted of only grassland and heathland. To determine the proportion of heathland and grassland over the landscape, the underlying soil type was used. First, two maps were obtained: New Forest broad habitat types map was obtained from the Hampshire Biodiversity Information Centre, Hampshire, used to identify grassland and heathland habitat areas initially (see Fig. 5.1); and a National Soil Map (NATMAP), obtained from National Soil Resources Institute, Silsoe. Second, the maps were combined and for each soil type, the percentage of heathland and grassland that it contained was calculated. If the soil type contained no heathland then that soil type was classified as only being able to become grassland (i.e. heathland species could not begin on or could not spread to that soil type), and vice versa. If the soil type underlay both types of habitat, the habitat that made up most percentage of its area was what the habitat it was assigned as. Any woodland initially present from the current maps was then reclassified as either heathland or grassland, resulting in the final 0% WC map.

5.3.4. Modelling framework

The spatially-explicit LANDIS-II (Scheller et al. 2007) landscape forest model (v6.0) was used in this study to simulate the spatiotemporal dynamics of the New Forest. The model has been used extensively throughout North America (Steenberg et al. 2011; Scheller et al. 2011) and has been used previously in the current study area, the New Forest (Cantarello et al. 2011; Newton et al. 2013; Cantarello et al. in press). LANDIS-II is a landscape model that simulates succession and disturbance over a landscape represented as a grid of interconnected cells of a user-defined size. In LANDIS-II, trees grow in cohorts grouped by species and age, not individually (Scheller et al. 2007). Climate data for all simulations were based on local monthly mean temperature and precipitation amounts from 1957-2014 (recorded at Hurn, approximately 10 km from the New Forest; Met Office, 2015). The monthly climate data remained the same duration of the simulation, which was 170 years.

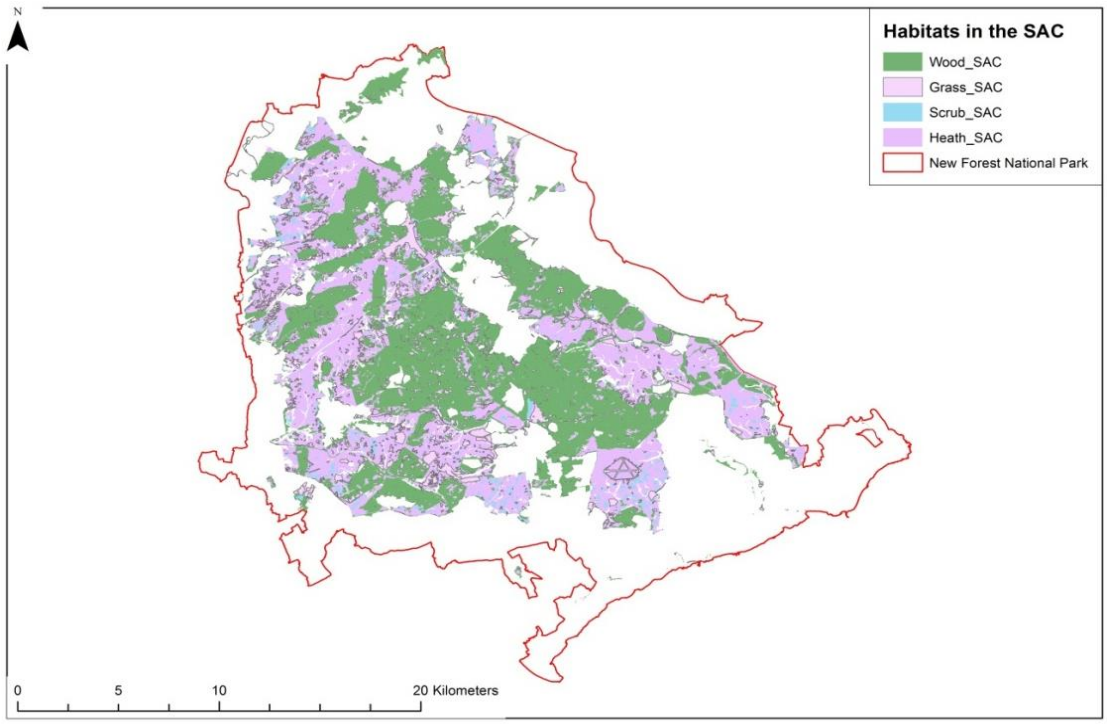

Fig. 5.1: Habitats of the New Forest Special Area of Conservation (SAC). The woodland (green), grassland (pink), scrubland (blue) and heathland (purple) habitats of the New Forest SAC. The habitat shapefiles were extracted from the Hampshire Biodiversity Information Centre landcover map.

5.3.5. Modelling parametrisation

The New Forest SAC has been parameterised for LANDIS-II in a previous study (Newton et al. 2013). More information can be found in that study; however, the important model parameterisation information is displayed here. The base LANDIS-II model requires raster landscape maps for determining the initial composition of the landscape - an ecoregion map, which describes different ecological conditions over the landscape, and an initial community map. The ecoregion map was classified into 25 active ecoregions based on homogenous soil type, topography and elevation data obtained from fieldwork, as described in Newton et al. (2013). The creation of the unique initial community maps is described above. These describe the community data of species and age cohorts present at the start of each simulation. Maps always excluded locations that incorporate water bodies, horticulture and arable field and urban development.

In LANDIS-II, all the species (i.e. trees) and the landscape require parameterisation. For each species, specific life history parameter requirements were taken from the literature (Burns and Honkala 1990; Escudero et al. 1992; Sjöström, 1993; Reich et al. 1996; Mediavilla and Escudero, 2003; Pyatt et al. 2003; Hill et al. 2004; Ishii et al. 2009; Wang et al. 2010; Scheller et al. 2012; Post and Pastor, 2013) and supplemented by field data collection. Life history traits determined the successional

dynamics of each species during the establishment phase of each timestep of the simulation. They included attributes such as fire tolerance, drought tolerance, shade tolerance, dispersal distance and average plant longevity. The probability of establishment of each species at each timestep depends on moisture and temperature conditions, as well as competition from other species. Overall, 30 woodland tree species were used in this study. For the input species parameters used in this study, see Appendix 5.1.

5.3.6. Scenarios

Each simulation was run for 170 years, from 2016-2186. Each pulse disturbance was activated at the timestep of 19 – 20 years (with the exception of the no pulse disturbance simulations), and then never again in the same simulation. When press disturbances were active, they began at 20 years and remained for the duration of the simulation.

5.3.6.1.Pulse disturbance

The Base Harvest extension (v2.0) of LANDIS-II was used to simulate the landscape effects of pulse and press disturbances. The five sets of PDI scenarios involved different intensities of one-time disturbance events. The five scenarios involved elimination of one or more locally important tree species: oak only (PDI1); beech only (PDI2); beech and oak (PDI3); beech, oak, holly and birch (PDI4); and no species (PDI0). In reality, extreme drought or pathogen attacks could have this effect; sudden oak death in the USA and ash dieback in Europe are recent examples of similar phenomena (Kowalski, 2006; Cunniffe et al. 2016). Once a species was removed, it was not present for the remainder of the simulation – it could not recolonise or regenerate.

5.3.6.2. Press disturbance

To determine whether additional press disturbances had an effect on landscape resilience further, all PDI scenarios were repeated with the inclusion of a press disturbance. In this study, the press disturbance was used to represent the effect of a high density of herbivores, based on literature-derived palatability of tree species to different animals present in the New Forest (Newton et al. 2013). For the press disturbance, four herbivory browsing categories were used: three deer (high-, med- and low-deer) and one pony (pony_browse). Herbivory categories consisted of different percentages of ‘harvesting’ of the categorised tree species juveniles (1 – 10 years old) (see CD, CD5.1 for parameters

used). Tree species in the high-deer category were harvested by 90%, in med-deer by 80% and in low-deer by 70%. For the pony browsing category, all involved species were harvested by 50%. The harvest area of each of these was set to 20% of the entire landscape, selected randomly at each timestep, for each individual browsing category. For illustration, 70% of all tree species juveniles in the low-deer category would have been harvested (eaten) in the randomly-selected 20% of the landscape. Meanwhile (i.e. in the same timestep), 80% of all tree species juveniles in the med-deer category would have been harvested in a different, but potentially-overlapping, set of cells which make up 20% of the landscape. Press disturbances were enacted continually from 21 years until the end of each scenario that included a press disturbance.

5.3.7. Carbon and nitrogen simulations

The dynamics of aboveground and belowground C and N were modelled using the Century Succession (v4.0) extension for LANDIS-II (Scheller et al. 2011). The extension is based on the original CENTURY soil model (Parton et al. 1983). For detailed information on the carbon and nitrogen flows in Century, see Scheller et al. (2008, 2011, 2012) and Lucash et al. (2014). The Century extension required species-specific, functional groups and ecoregions inputs. The Century extension was calibrated following Scheller et al. (2011a) and Loudermilk et al. (2013), and is explained in detail for the New Forest in Cantarello et al. (in press). Briefly, the net ecosystem exchange (NEE), a measurement of carbon uptake, was modelled against empirical data collected at Alice Holt flux tower (51º9'13'' N 0º51'30'' W), which gave a result of r^2 of 0.77. The initial aboveground biomass and the accumulation of biomass were calibrated using data from previous New Forest studies (Cantarello and Newton, 2008; Newton et al. 2013; Chapter 2 of this thesis).

5.3.8. Ecosystem properties

Ten EPs were assessed in this study (Table 5.1). They consisted of biodiversity, ES and ecosystem function metrics that are important in temperate woodlands. These were: species richness of ectomycorrhizal fungi (ECM), vascular ground flora (GF), epiphytic lichen and tree species (for all richness measures, the units are number of unique species ha^{-1}); aboveground biomass (AGB) (Mg ha^{-1}); net mineralisation [(µg NO_3^- + NH_4^+) $capsule^{-1}$)]; soil respiration rate (µmols m^2 s^{-1}); soil nitrogen stock (Mg N ha^{-1}); timber volume (m^3 ha^{-1}); and total carbon stock (Mg C ha^{-1}). Net mineralisation, the soil respiration rate and most biodiversity metrics, with the exception of tree species richness,

were derived from the results in the study in Chapter 2 of this thesis. The values for AGB, total C stock, and soil N stock were calculated from the LANDIS-II Century extension output, and timber volume was calculated by multiplying the aboveground biomass of important timber species (beech and oak in this study) using respective nominal specific gravity (Jenkins et al. 2011). All values were calculated at the stand scale, and then averaged over the whole landscape.

For EPs calculated from Chapter 2's results, generalised linear models (GLMs) were used to fit each of the variables against AGB of broadleaved trees. For each variable, null, linear and non-linear relationships between AGB and the individual EP variable were modelled. All species richness measures were modelled with a Poisson error structure as they were count data (i.e. non-negative integers). Gaussian errors were used for the other variables. The outputs of all the three models were then averaged, based on the relative weight of each model, using the MuMIn package (Barton, 2015). The resulting averaged coefficients were used to determine a value for each variable at each timestep (i.e. every 5 years). This value was averaged for each ecoregion of the model, and each EP value obtained.

Data analysis

5.3.8.1. Woodland cover and connectivity correlations

To determine if significant relationships existed between WC, the proxy connectivity measure used in this study, and other common connectivity measures, spatial outputs at every 10 years of all simulations were input into Fragstats (v4.2) (McGarigal, 2015), a spatial analysis programme that calculates numerous connectivity metrics. Bonferroni-corrected Spearman Rank correlation tests were then carried out on Fragstats output, which was used to analyse total patch area (i.e. WC) against other connectivity measures.

5.3.8.2. Resilience attribute measurements

From the LANDIS-II outputs, the values of all EPs were averaged across the landscape, to show their value at stand scale. To be able to assess all EPs on the same scale, the individual resilience attributes were converted into either proportions (resistance and persistence) or recorded as time taken for the EP to equal its pre-disturbance value (recovery). Consequently, following Shade et al. (2012), resistance was measured as the proportion difference between 15 years, the last value recorded before the pulse disturbance, and 20 years, the first value recorded after the pulse disturbance (Eq. 1). Thus,

(Eq. 1) Resistance = $1 - \frac{2\,|y_{15} - y_{20}|}{y_{15} + |y_{15} - y_{20}|}$

where y_{15} and y_{20} are the EP values at year 15 (the pre-disturbance value) and year 20 (the value immediately following the pulse disturbance), respectively.

Persistence was measured as proportion regained of the EP value by the end of the simulation. This was calculated by dividing the value at the final timestep (i.e. 170 years) from the last recorded timestep before the perturbation (i.e. 15 years) (Eq. 2). As the persistence value was the proportion regained, any values which were > 1 (i.e. cases where the EP value ended higher than it began) were capped at 1. Thus,

(Eq. 2) Persistence = $\left| \frac{y_{170}}{y_{15}} \right|$

where y_{170} is the EP value at 170 (the final value), 150 years after the pulse disturbance. The recovery time was measured as the first year after the pulse disturbance that the EP value was equal or greater than the pre-disturbance EP value (Eq. 3). Thus,

(Eq. 3) Recovery time (r) = $y_{r \geq} y_{15}$

where *r* is the year (timestep). If an EP value never fully recovered, it was given a value of 150, the maximum length of time of the simulation subsequent to the pulse disturbance.

5.3.8.3.PDI scenario GLMs

The results of each of the five PDI scenarios were analysed separately using GLMs to determine whether WC had an effect on resilience in response to the different pulse disturbance intensities. For each PDI scenario, a specific resilience attribute (resistance, persistence or recovery) was used as the dependent variable. As resistance and persistence were recorded as proportions – i.e. all values were continuous and bounded between 0 and 1 - beta regression models were initially fitted, following Ferrari and Cribari-Neto (2004), using the *betareg* r package (Zeileis et al. 2016). As resistance and persistence sometimes included the extremes of 0 and 1, resistance and persistence models were transformed following Smithson and Verkuilen (2006; see (Eq. 4)).

(Eq. 4) Transformation for beta regression = $(y * (n - 1) + 0.5)/n$

where n is the sample size and y is the dependent variable. For ease of interpretation, resistance and persistence results were converted to percentages subsequently. To determine the best-fitting model for recovery, GLMs were fitted using a Poisson error structure, as the data were non-negative integers.

To determine what the relationship for each EP to the different resilience attributes was, null models and models with linear and quadratic terms of initial WC were fitted, with and without the effects of herbivory. Linear and quadratic terms describing the shape of the resilience relationship with WC were tested to identify any potential linearity or non-linearity, as both types of relationship have been predicted to exist between WC and resilience (Grêt-Regamey et al. 2014; Tambosi et al. 2014; Altieri et al. 2015; Mitchell et al. 2015). The most parsimonious model was chosen using model selection based on the lowest AIC values of each set of models, corrected for small sample sizes, using the MuMin package (Barton, 2015). The effect of WC on the resilient attributes were only considered to be substantial if the met *a priori* criteria of the most parsimonious model having $\Delta AIC > 4$ from the null model and if the $r^2 > 0.4$.

Finally, to determine whether there were significant relationships between the three resilience attributes under each PDI scenario, Spearman Rank correlations were used to calculate how related each final value of the resilient attributes were to each other attribute individually. The correlation analyses were calculated using the endpoint mean resilient attribute values from the six simulations of each PDI scenario, i.e. three from each of the repeated simulations with and without press disturbance. The simulations with and without press disturbance where also analysed separately. Correlations could not be calculated for EPs that were either always resistant or that consistently recovered fully, regardless of initial WC in a PDI scenario. All statistical analyses were conducted in R 3.2.3. (R Development Core Team, 2015, http://www.r-project.org/).

Table 5.1: Summary of ecosystem properties assessed. Type indicates whether the metric was biodiversity, an ecosystem function or an ecosystem service (ES). The 'calculated from' column specifies whether the final ecosystem property values were obtained based on the aboveground biomass (AGB) of broadleaved trees, taken from Chapter 2's results, or directly from LANDIS-II outputs based on species interactions.

Ecosystem property	Type	Abbreviation	Units	Calculated from
Aboveground biomass	Ecosystem function	AGB	Mg ha^{-1}	LANDIS-II outputs
Ectomycorrhizal fungi	Biodiversity	ECM	No. of unique species ha^{-1}	Relationship with AGB
Net mineralisation	Ecosystem function	Net min	[(µg NO_3^- + NH_4^+) $capsule^{-1}$)]	Relationship with AGB
Soil respiration rate	Ecosystem function	SRR	µmols m^2 s^{-1}	Relationship with AGB
Total carbon stock	ES	Carbon	Mg C ha^{-1}	LANDIS-II outputs
Total nitrogen stock	ES	Nitrogen	Mg N ha^{-1}	LANDIS-II outputs
Timber volume	ES	Timber	m^3 ha^{-1}	LANDIS-II outputs
Tree species richness	Biodiversity	Tree species	No. of unique species ha^{-1}	Relationship with AGB
Ground flora species richness	Biodiversity	GF	No. of unique species ha^{-1}	Relationship with AGB
Epiphytic lichen species richness	Biodiversity	Lichen	No. of unique species ha^{-1}	Relationship with AGB

5.4. Results

5.4.1. PDI impacts on aboveground biomass

AGB showed a mean reduction of 22.40% (29.690 Mg ha^{-1}) overall, with mean AGB changing due to disturbance an average of -12.776% (-12.407 Mg ha^{-1}) in scenario PDI1, -18.334% (-29.054 Mg ha^{-1}) under PDI2, -38.138% (-50.234 Mg ha^{-1}) under PDI3, and -47.356% (-61.649 Mg ha^{-1}) under PDI4. However, there were large variations between the initial WC stages (Fig 5.2; Table A5.7). In terms of percentage AGB change under PDI scenarios that featured a disturbance (i.e. not PDI0), 25% WC almost always declined the most out of all the initial WC stages, with the exception of the PDI2 scenario. Unsurprisingly, most WC stages lost increasing amounts of AGB as the intensity of disturbance increased. This was with the exception of 25% WC where AGB declined more under PDI1 than PDI2.

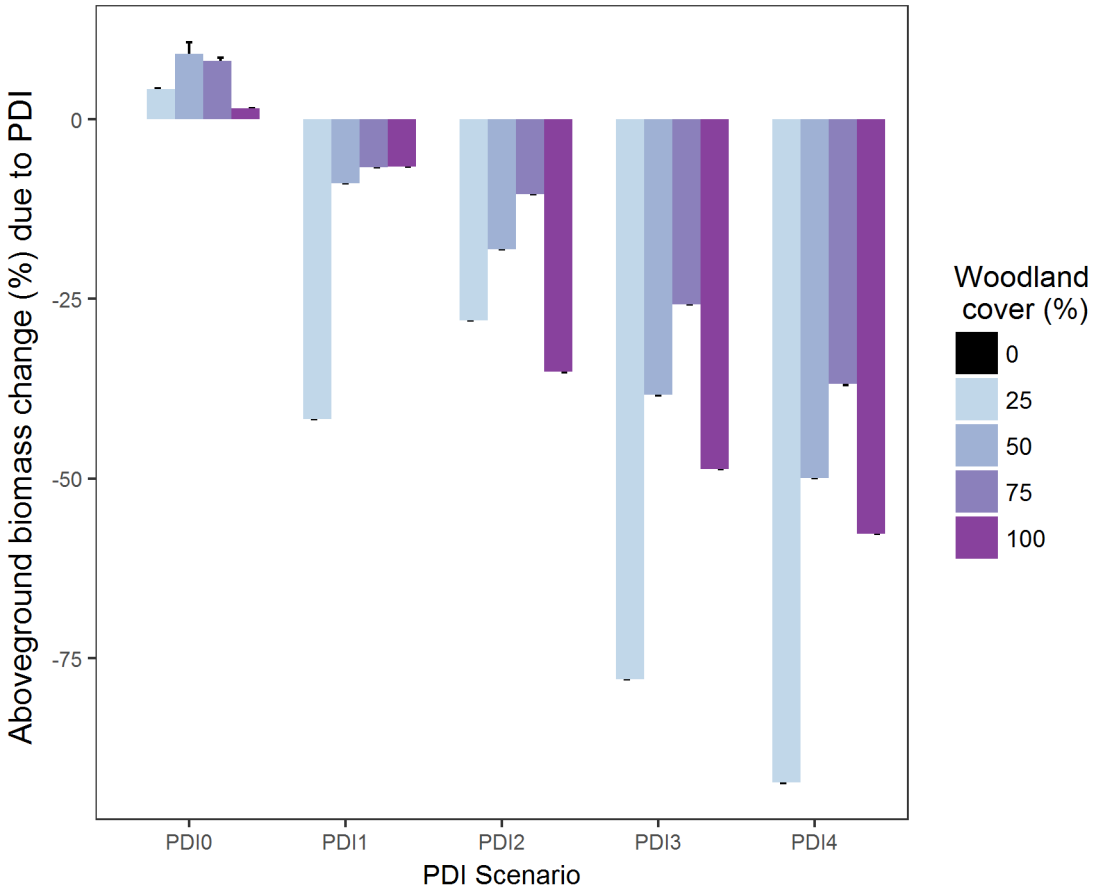

Fig. 5.2: Mean changes in aboveground biomass resulting from the different pulse disturbance intensity (PDI) scenarios. The coloured bars represent the mean percent change of woodland cover under the different PDI scenarios. The black lines represent the standard deviations of the means. Note: 0% WC cannot be seen as it did not change. The five sets of PDI scenarios involved different intensities of one-time disturbance events, which were carried out through the elimination of one or more locally important tree species: oak only (PDI1); beech only (PDI2); beech and oak (PDI3); beech, oak, holly and birch (PDI4); and no species (PDI0).

5.4.2. Woodland cover related to other connectivity metrics

WC was highly positively correlated with other common measures of connectivity, including mean patch area (r = 0.964, P < 0.001, r^2 = 0.929); the mean spatial connectedness of the habitat, the contiguity index (r = 0.627, P < 0.001, r^2 = 0.393); physical connectedness, patch cohesion (r = 0.959, P < 0.001, r^2 = 0.920); and the mean similarity (r = 0.469, P < 0.001, r^2 = 0.220). See CD, CD5.2 for connectivity correlation results.

5.4.3. Effect of woodland cover on resistance

WC had an effect on the resistance of three EPs under the PDI1 and five EPs for PDI2, PDI3 and PDI4. Thus, WC influenced the resistance of 18/40 EPs altogether when there was a pulse disturbance. Timber volume and tree species richness were the only EPs to exhibit non-linear relationships to resistance when there was a pulse disturbance. In scenario PDI1 (Fig 5.3; Table 5.2) and PDI2 (Fig 5.4; Table 5.2), tree species exhibited a negative relationship with WC, becoming steeper over the latter stages, while tree species under PDI3 (Fig 5.5; Table 5.2) and PDI4 (Fig 5.6; Table 5.2) had an upwards-facing concave relationship with WC, where tree species resistance increased after the 50% WC stage. For timber under PDI3 and PDI4 (Figs 5.5-5.6; Table 5.2), resistance was 0 for all WC stages other than 0% WC, creating a sharp decline between 0% and 25% WC and followed by a plateau at 0% resistance. For timber under PDI1 and PDI2, resistance initially declined followed by an increase after the 50% WC (r^2_{adj} = 0.774; ΔAIC = 14.787) and the 75% WC stages (r^2_{adj} = 0.888; ΔAIC = 11.131), respectively (Figs 5.3 – 5.6; Table 5.2). When there was no pulse disturbance (i.e. PDI0), WC had a significant effect on four EPs between 15 and 20 years.

Table 5.2: The most parsimonious models for resistance and associated measures of parsimony (Log likelihood, AIC), support (ΔAIC, AIC weight) and goodness of fit (r^2_{adj}). WC and WC^2 indicate that linear and quadratic terms of woodland cover were used in the most parsimonious models, respectively. Null indicates that the null model was the most parsimonious. PDI indicates the intensity of disturbance the resistance of the ecosystem properties was measured in response to.

Resistance					
Ecosystem property	**Model structure**	**Log likelihood**	**ΔAIC**	**AIC Weight**	r^2_{adj}
PDI1					
AGB	Null	-57.173	8.138	0.978	0
Carbon	Null	-49.155	10.898	0.996	0
ECM	Null	-44.992	7.134	0.972	0
GF	Null	955.942	93.026	1	0
Lichen	Null	-36.45	11.794	0.997	0
Net min	Null	955.942	93.026	1	0
Nitrogen	WC	6.184	4.226	0.892	0.479
SRR	Null	-18.596	13.019	0.999	0
Timber	$WC+WC^2$	-52.732	14.787	0.999	0.774
Tree species	WC	-42.755	7.479	0.975	0.472
PDI2					
AGB	WC	-53.8	7.461	0.957	0.465
Carbon	WC	-47.54	3.597	0.857	0.394
ECM	WC	-41.078	16.634	1	0.638
GF	Null	955.942	93.026	1	0
Lichen	WC	-33.777	14.288	0.999	0.592
Net min	Null	955.942	93.026	1	0
Nitrogen	WC	32.444	26.196	0.748	0.769
SRR	WC	-34.476	3.782	0.828	0.454
Timber	$WC+WC^2$	-47.27	11.131	0.996	0.888
Tree species	Null	-44.534	2.024	0.662	0
PDI3					
AGB	Null	-66.927	0.695	0.543	0
Carbon	WC	-53.742	2.738	0.743	0.367
ECM	WC	-49.236	9.69	0.99	0.542
GF	Null	955.942	93.026	1	0
Lichen	WC	-42.795	8.833	0.986	0.498
Net min	Null	955.942	93.026	1	0
Nitrogen	Null	-17.79	4.496	0.904	0
SRR	WC	-31.812	12.38	0.998	0.567
Timber	$WC+WC^2$	-65.064	29.336	1	0.892
Tree species	$WC+WC^2$	-35.708	8.992	0.989	0.833
PDI4					

AGB	Null	-70.942	2.823	0.772	0
Carbon	WC	-54.963	1.602	0.637	0.396
ECM	WC	-50.077	7.28	0.973	0.567
GF	Null	955.942	93.026	1	0
Lichen	WC	-43.748	9.219	0.987	0.536
Net min	Null	955.942	93.026	1	0
Nitrogen	Null	-21.761	12.8	0.998	0
SRR	WC	-30.482	17.984	1	0.643
Timber	$WC+WC^2$	-70.54	17.921	1	0.848
Tree species	$WC+WC^2$	-17.815	49.982	1	0.966
PDI0					
AGB	Null	955.942	93.026	1	0
Carbon	Null	955.942	93.026	1	0
ECM	Null	955.942	93.026	1	0
GF	$WC+WC^2$	-16.472	12.693	0.998	0.853
Lichen	Null	955.942	93.026	1`	0
Net min	WC	-10.451	12.855	0.998	0.674
Nitrogen	$WC+WC^2$	29.349	9.064	0.987	0.838
SRR	Null	955.942	93.026	1	0
Timber	Null	955.942	93.026	1	0
Tree species	WC	-43.401	6.124	0.955	0.449

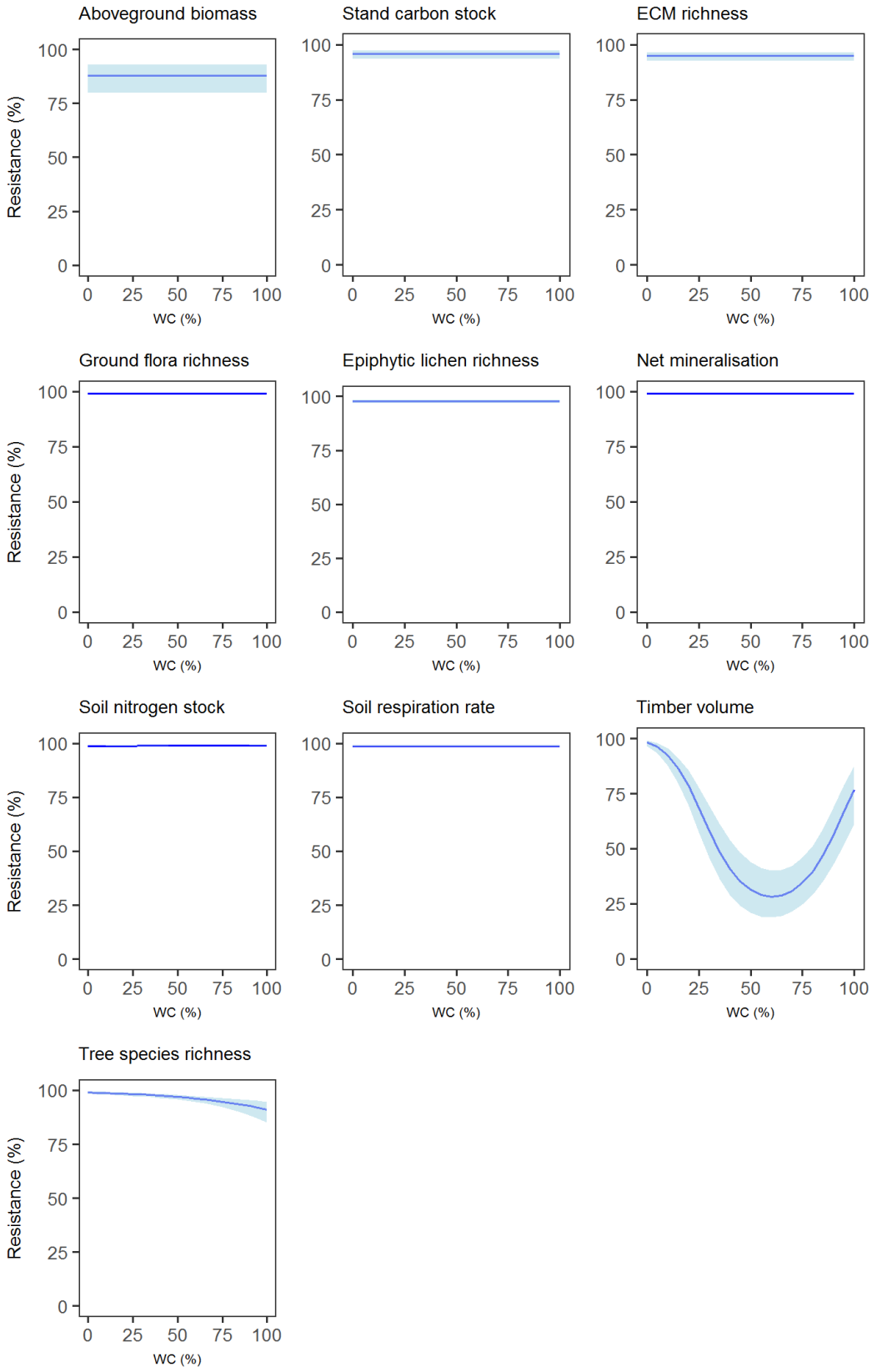

Fig. 5.3. Results of the most parsimonious GLMs for resistance of the different ecosystem properties across the woodland cover (WC) gradient resulting from PDI1. The blue lines represent the most parsimonious model for all EPs, and the blue surrounds represent the 95% confidence intervals of the most parsimonious model.

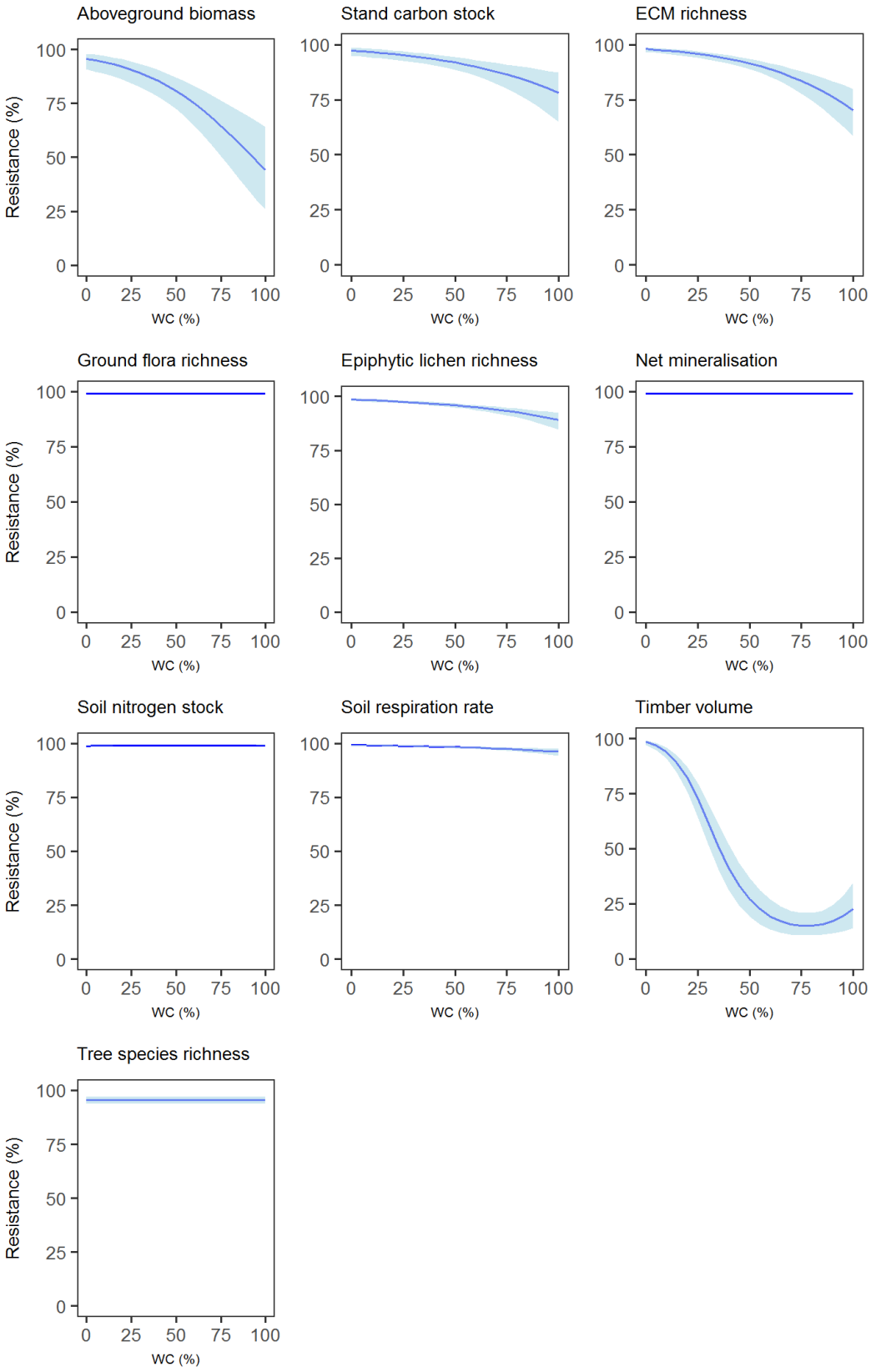

Fig. 5.4. Results of the most parsimonious GLMs for resistance of the different ecosystem properties across the woodland cover (WC) gradient resulting from PDI2. The blue lines represent the most parsimonious model for all EPs, and the blue surrounds represent the 95% confidence intervals of the most parsimonious model.

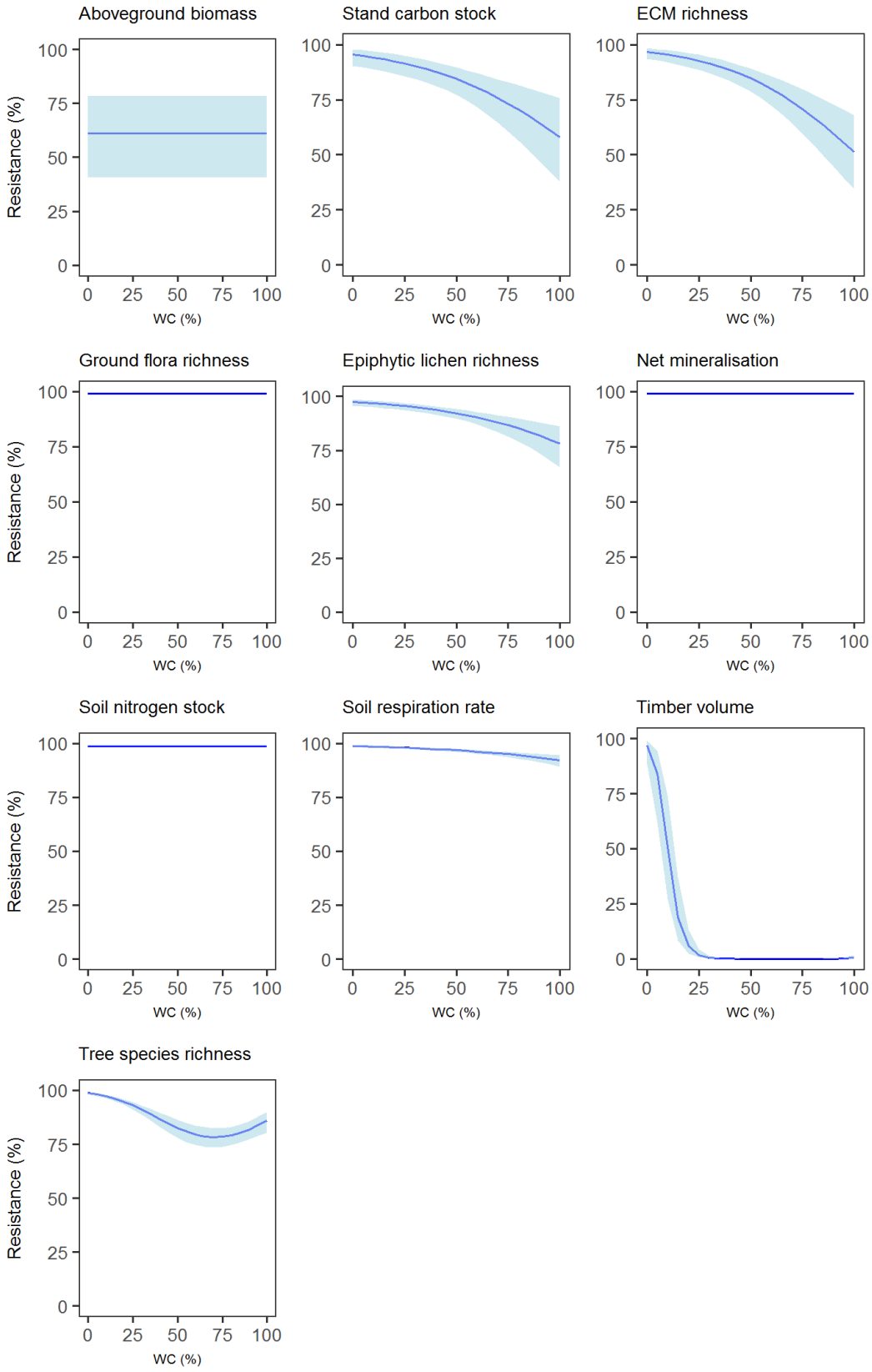

Fig. 5.5. Results of the most parsimonious GLMs for resistance of the different ecosystem properties across the woodland cover (WC) gradient resulting from PDI3. The blue lines represent the most parsimonious model for all EPs, and the blue surrounds represent the 95% confidence intervals of the most parsimonious model.

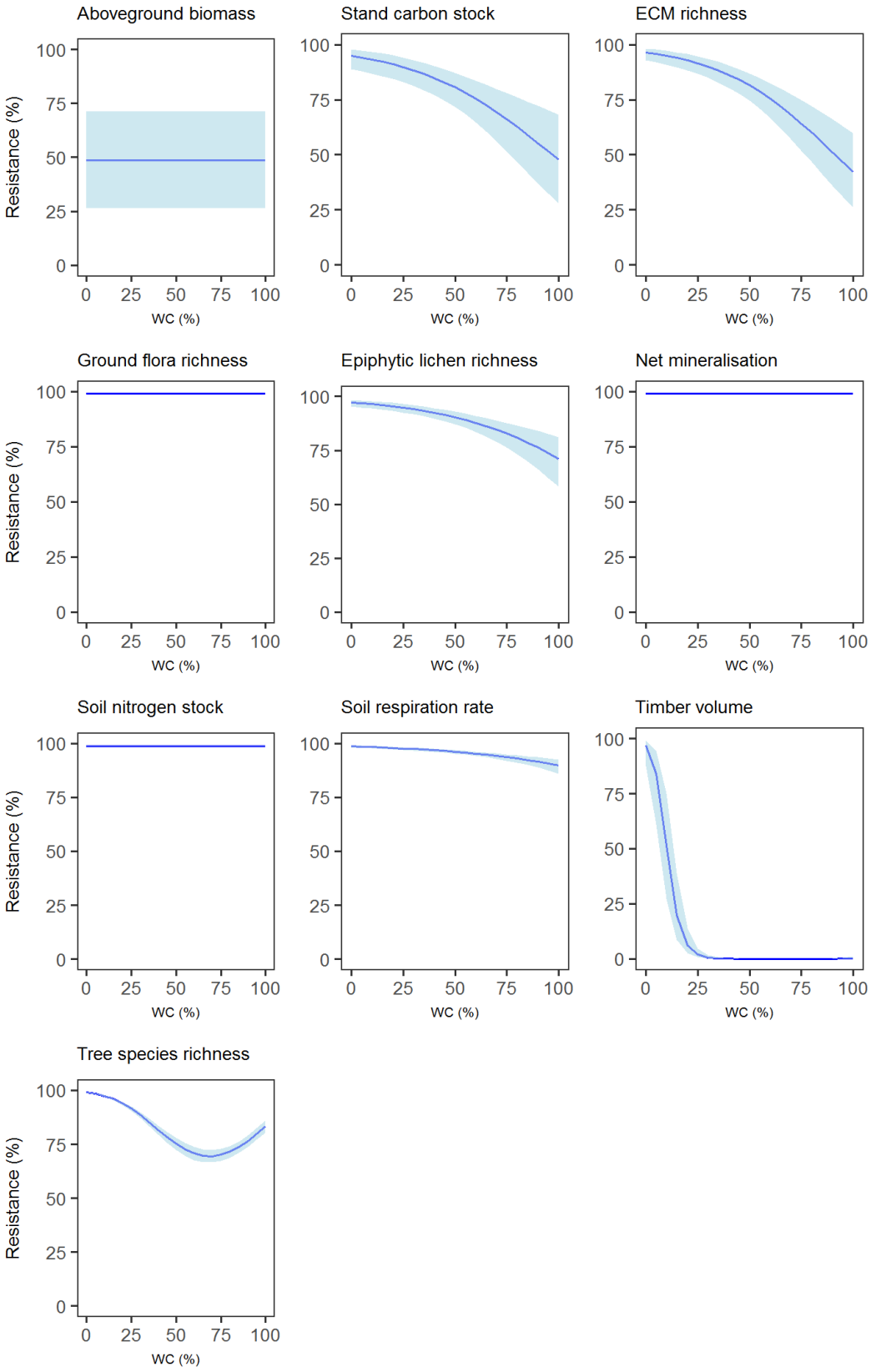

Fig. 5.6. Results of the most parsimonious GLMs for resistance of the different ecosystem properties across the woodland cover (WC) gradient resulting from PDI4. The blue lines represent the most parsimonious model for all EPs, and the blue surrounds represent the 95% confidence intervals of the most parsimonious model.

5.4.4. Effect of woodland cover on persistence

The initial WC had an effect on the persistence of four EPs under PDI1 scenario, six under PDI2, six under PDI3 and three EPs in the PDI4. Thus, WC influenced the resistance of 18/40 EPs altogether. When there was no pulse disturbance, WC had a significant effect on four EPs between 30 and 170 years (Table 5.3; Figs 5.7–5.10).

Table 5.3: The most parsimonious models for persistence and associated measures of parsimony (Log likelihood, AIC), support (ΔAIC, AIC weight) and goodness of fit (r^2_{adj}). WC and WC^2 indicate that linear and quadratic terms of woodland cover were used in the most parsimonious models, respectively. H indicates that the press disturbance (i.e. herbivory) was included as a term in the most parsimonious model. Null indicates that the null model was the most parsimonious. PDI indicates the intensity of disturbance the ecosystem properties were measured in response to.

Persistence					
Ecosystem property	**Model structure**	**Log likelihood**	**ΔAIC**	**AIC Weight**	r^2_{adj}
PDI1					
AGB	Null	955.942	0	1	0
Carbon	Null	-27.304	0	0.573	0
ECM	Null	955.942	0	1	0
GF	$WC+WC^2+H$	-33.058	32.24	0.992	0.902
Lichen	Null	955.942	0	1	0
Net min	WC+H	-32.432	31.382	0.709	0.797
Nitrogen	$WC+WC^2$	-32.842	27.392	0.57	0.867
SRR	Null	955.942	0	1	0
Timber	Null	955.942	0	1	0
Tree species	$WC+WC^2$	-36.773	29.904	0.838	0.876
PDI2					
AGB	$WC+WC^2$	-43.318	8.017	0.519	0.729
Carbon	Null	-43.199	0	0.339	0
ECM	WC	-40.986	3.542	0.31	0.402
GF	$WC+WC^2+H$	-31.442	39.667	0.997	0.925
Lichen	Null	-30.531	0	0.51	0
Net min	$WC+WC^2+H$	-31.626	28.631	0.997	0.89
Nitrogen	$WC+WC^2$	-28.838	33.818	0.779	0.895
SRR	Null	-20.518	0	0.591	0
Timber	$WC+WC^2$	-44.147	20.566	0.824	0.822

Tree species	WC+WC^2	-32.026	37.065	0.92	0.905
PDI3					
AGB	H	-60.356	6.491	0.685	0.237
Carbon	H	-56.863	1.332	0.629	0.1
ECM	WC+H	-48.109	8.785	0.875	0.53
GF	H	-40.797	5.211	0.927	0.24
Lichen	WC+H	-36.991	11.104	0.944	0.589
Net min	H	-33.943	4.778	0.913	0.241
Nitrogen	WC	-34.941	30.783	0.535	0.767
SRR	WC	-29.431	6.383	0.372	0.472
Timber	WC+WC^2	-64.619	40.253	0.582	0.899
Tree species	WC+WC^2	-37.322	30.296	0.903	0.877
PDI4					
AGB	H	-65.259	4.288	0.845	0.169
Carbon	Null	-62.48	0	0.633	0
ECM	H	-54.78	3.065	0.508	0.155
GF	Null	-26.46	0	0.582	0
Lichen	H	-44.995	2.739	0.572	0.166
Net min	Null	-16.369	0	0.663	0
Nitrogen	WC	-37.87	29.19	0.851	0.752
SRR	WC	-31.144	3.118	0.487	0.408
Timber	WC+WC^2	-70.54	29.08	0.737	0.848
Tree species	WC+WC^2	-38.79	31.879	0.861	0.882
PDI0					
AGB	Null	955.942	0	1	0
Carbon	Null	955.942	0	1	0
ECM	Null	955.942	0	1	0
GF	WC+WC^2	-39.489	22.426	0.547	0.837
Lichen	Null	955.942	0	1	0
Net min	WC+WC^2+H	-33.965	22.72	0.633	0.863
Nitrogen	WC+WC^2	-34.03	23.63	0.915	0.848
SRR	Null	955.942	0	1	0
Timber	Null	955.942	0	1	0
Tree species	WC+WC^2	-38.67	28.625	0.887	0.869

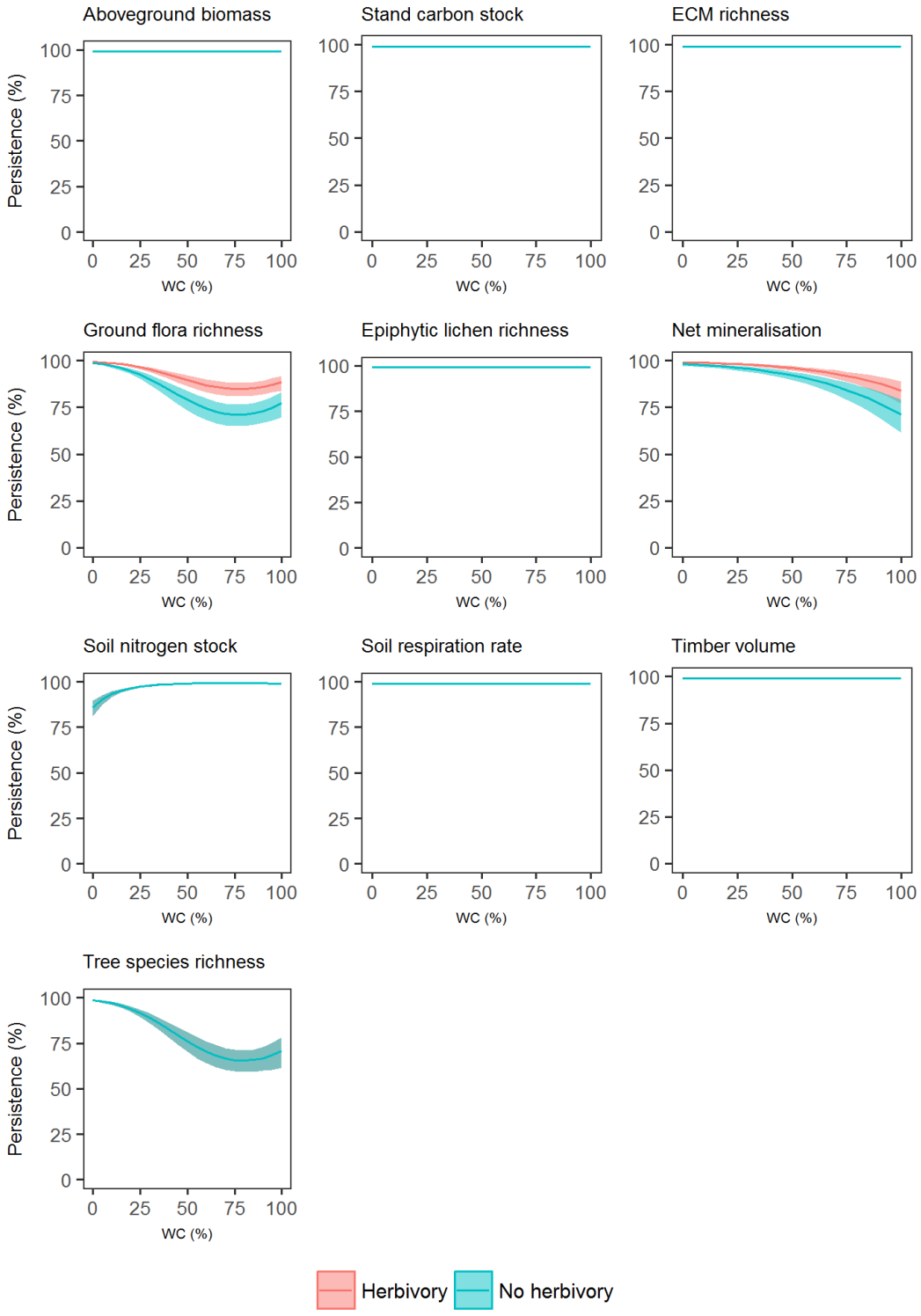

Fig. 5.7. Results of the most parsimonious GLMs for persistence of the different ecosystem properties across the woodland cover (WC) gradient resulting from PDI1. The red and blue lines and surrounds represent the most parsimonious model, with and without herbivory, respectively. The coloured surrounds represent the 95% confidence intervals of the most parsimonious model. Note: where herbivory did not have a significant effect in the most parsimonious model both lines and confidence intervals overlap, with the only the blue lines and surrounds showing.

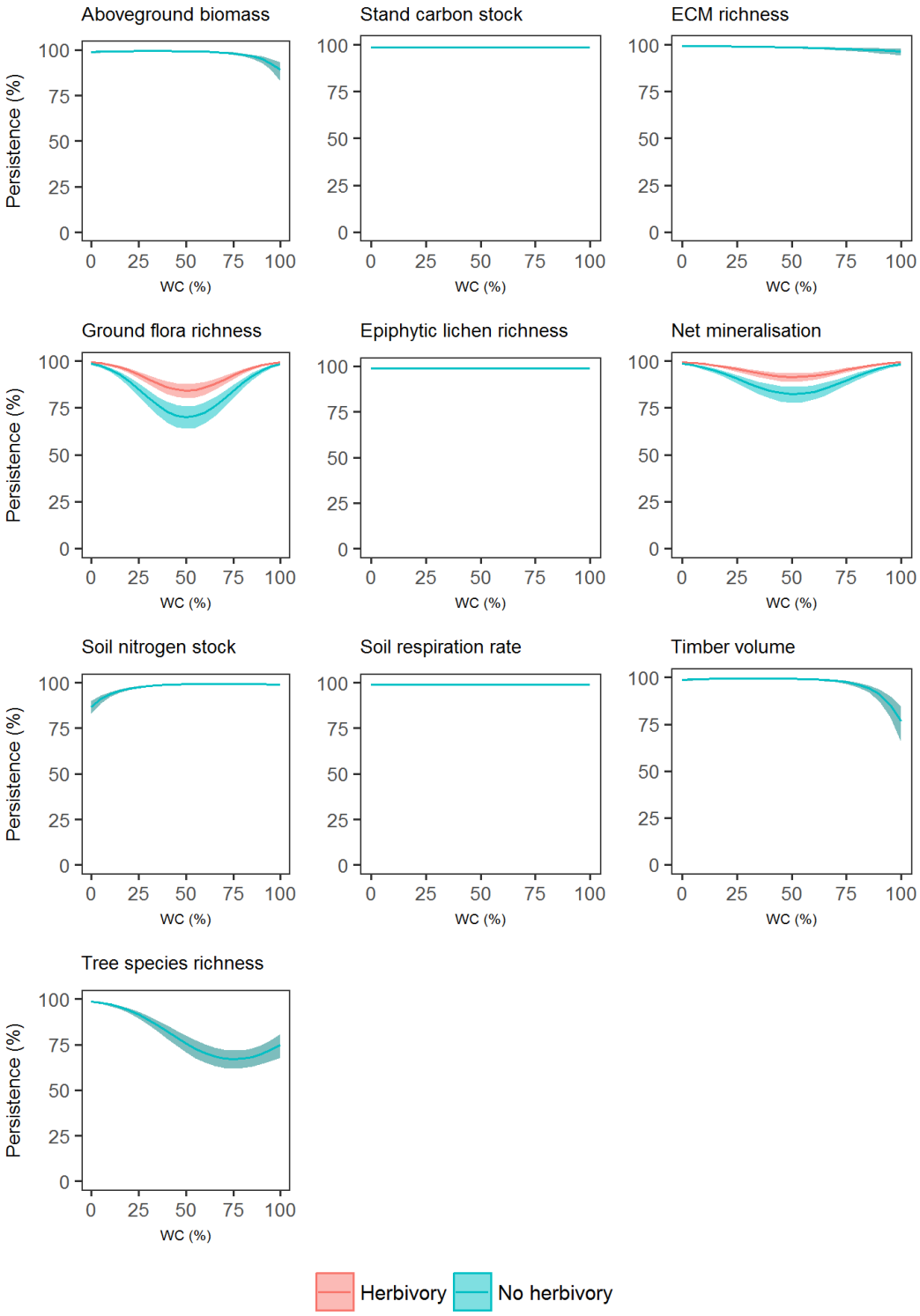

Fig. 5.8. Results of the most parsimonious GLMs for persistence of the different ecosystem properties across the woodland cover (WC) gradient resulting from PDI2. The red and blue lines and surrounds represent the most parsimonious model, with and without herbivory, respectively. The coloured surrounds represent the 95% confidence intervals of the most parsimonious model. Note: where herbivory did not have a significant effect in the most parsimonious model both lines and confidence intervals overlap, with the only the blue lines and surrounds showing.

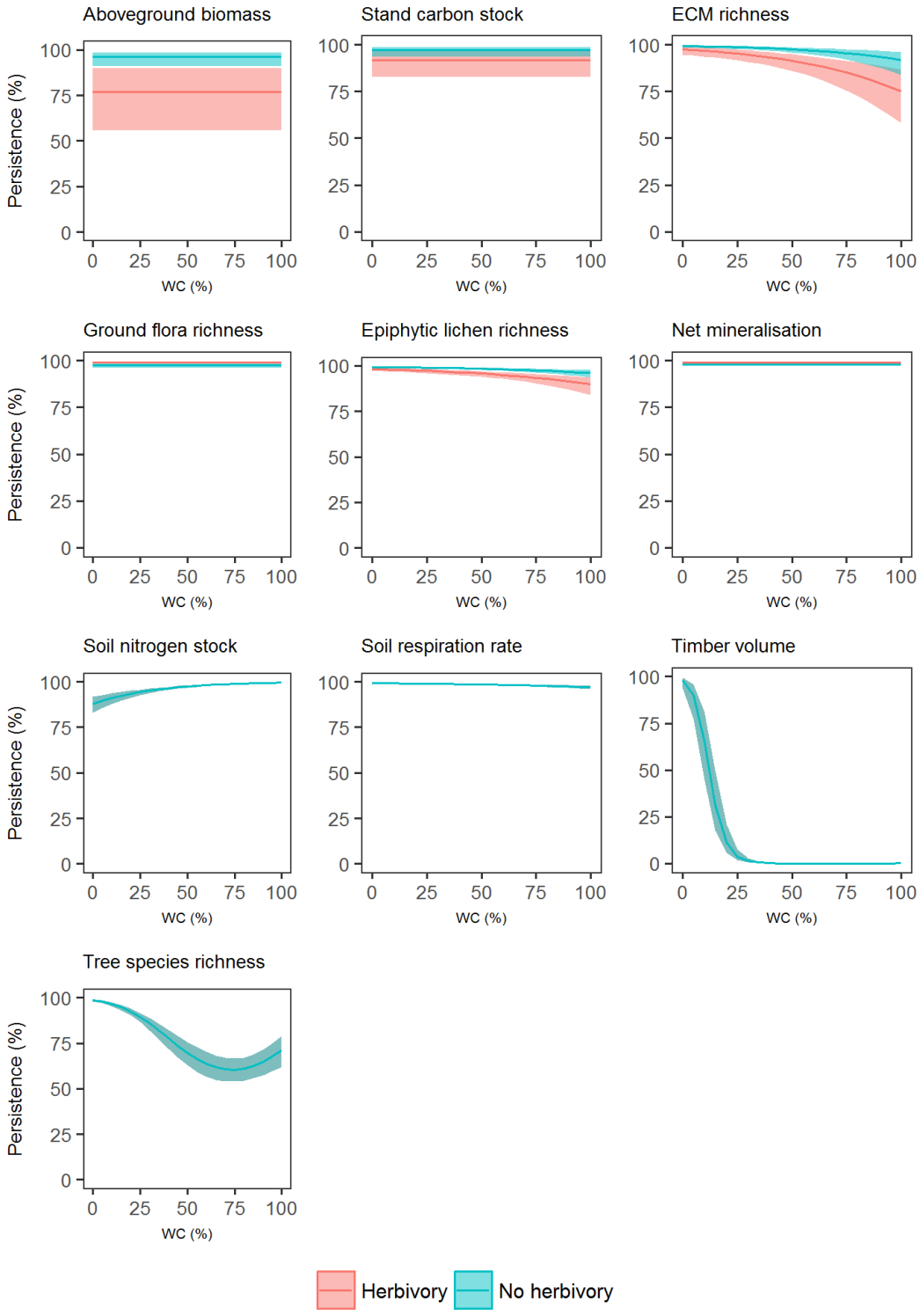

Fig. 5.9. Results of the most parsimonious GLMs for persistence of the different ecosystem properties across the woodland cover (WC) gradient resulting from PDI3. The red and blue lines and surrounds represent the most parsimonious model, with and without herbivory, respectively. The coloured surrounds represent the 95% confidence intervals of the most parsimonious model. Note: where herbivory did not have a significant effect in the most parsimonious model both lines and confidence intervals overlap, with the only the blue lines and surrounds showing.

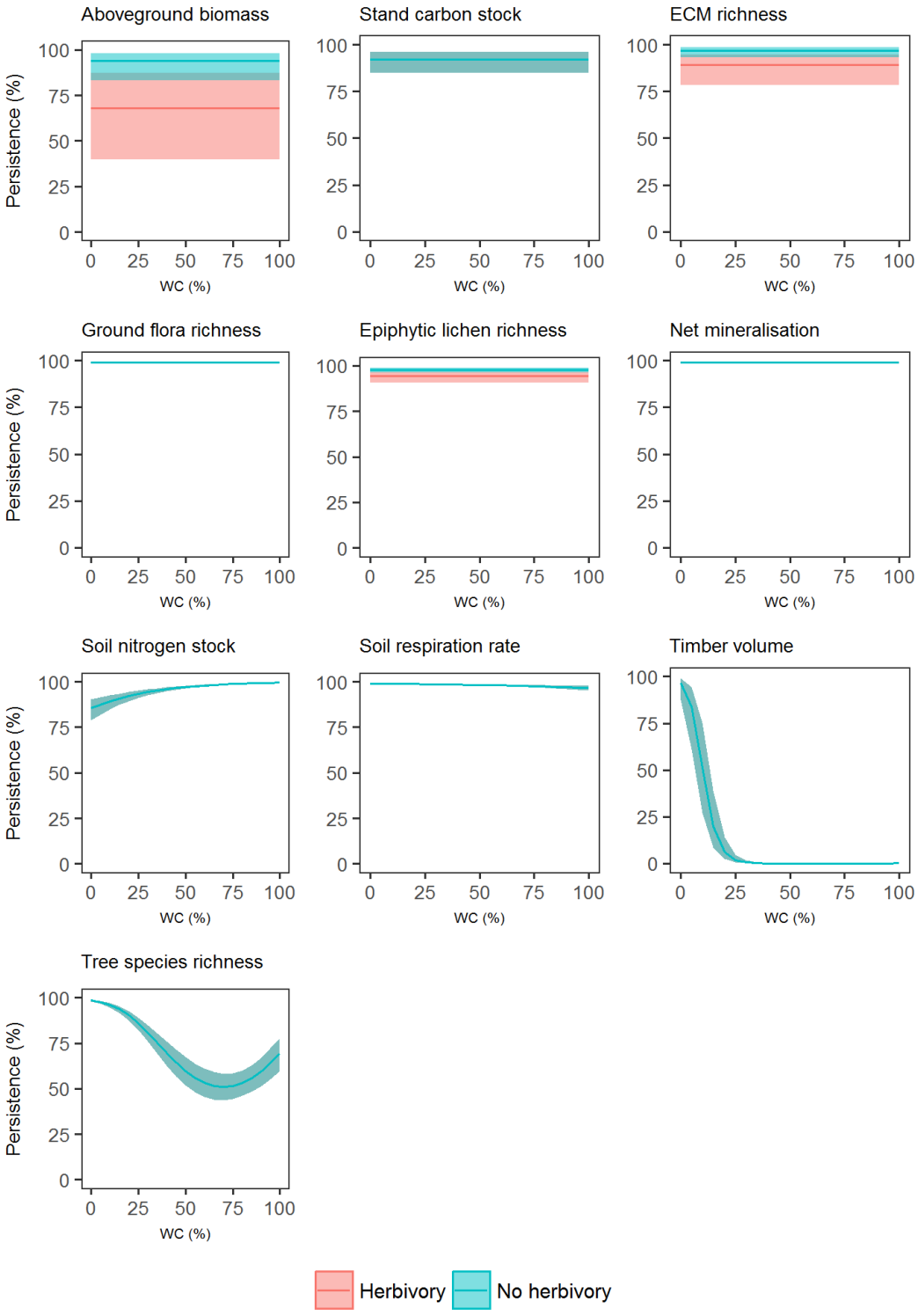

Fig. 5.10. Results of the most parsimonious GLMs for persistence of the different ecosystem properties across the woodland cover (WC) gradient resulting from PDI4. The red and blue lines and surrounds represent the most parsimonious model, with and without herbivory, respectively. The coloured surrounds represent the 95% confidence intervals of the most parsimonious model. Note: where herbivory did not have a significant effect in the most parsimonious model both lines and confidence intervals overlap, with the only the blue lines and surrounds showing.

5.4.5. Effect of woodland cover on recovery

The initial WC had an effect on the recovery time of 10 EPs in both PDI1 and PDI2, and eight EPs for PDI3 and PDI4. Thus, WC influenced the recovery of 36/40 EPs altogether. For PDI4, there was a sharp increase for EPs that were influenced by WC between the 0% and 25% WC, after which most reached the maximum recovery time (i.e. 150 years) when herbivory was significant. WC influenced the trajectory of four EPs when there was no pulse disturbance (Table 5.4; Figs 5.11–5.14).

Table 5.4: The most parsimonious models for recovery time fitted and associated measures of parsimony (Log likelihood, AIC), support (ΔAIC, AIC weight) and goodness of fit (r^2_{adj}). WC and WC^2 indicate that linear and quadratic terms of woodland cover were used in the most parsimonious models, respectively. H indicates that the press disturbance (i.e. herbivory) was included as a term in the most parsimonious model. WC*H indicates that a significant interaction between WC and herbivory was included in the most parsimonious model. Null indicates that the null model was the most parsimonious. PDI indicates the intensity of disturbance that the response of the ecosystem properties was measured in response to.

Recovery					
Ecosystem property	**Model structure**	**Log likelihood**	**ΔAIC**	**AIC Weight**	r^2_{adj}
PDI1					
AGB	$WC+WC^2+H$	-372.406	175.699	0.791	0.015
Carbon	$WC+WC^2+H$	-231.454	1632.383	0.704	0.308
ECM	$WC+WC^2+H$	-372.406	175.699	0.791	0.015
GF	$WC*H+WC^2$	-337.178	2509.58	1	0.661
Lichen	$WC+WC^2+H$	-372.406	175.699	0.791	0.015
Net min	$WC*H+WC^2$	-337.178	2509.58	1	0.661
Nitrogen	$WC*H+WC^2$	-164.309	2744.436	0.481	0.824
SRR	$WC+WC^2+H$	-372.406	175.699	0.791	0.015
Timber	$WC+WC^2$	-399.96	349.988	0.759	0.408
Tree species	$WC*H+WC^2$	-419.675	1266.088	1	0.835
PDI2					
AGB	$WC*H+WC^2$	-272.679	1598.274	0.605	0.435
Carbon	$WC*H+WC^2$	-654.13	985.478	0.992	0.159
ECM	$WC*H+WC^2$	-272.679	1598.274	0.605	0.435
GF	$WC*H+WC^2$	-187.319	2766.322	1	0.465
Lichen	$WC*H+WC^2$	-316.712	1650.706	0.536	0.28
Net min	$WC*H+WC^2$	-198.836	1536.173	1	0.289
Nitrogen	$WC*H+WC^2$	-162.384	2706.036	0.86	0.827

SRR	$WC*H+WC^2$	-272.679	1598.274	0.605	0.435
Timber	WC*H	-204.976	1096.546	0.393	0.758
Tree species	$WC+WC^2$	-378.595	951.22	0.779	0.839
PDI3					
AGB	$WC+WC^2+H$	-780.923	513.709	0.535	0.597
Carbon	WC+H	-1004.181	224.789	0.375	0.319
ECM	$WC+WC^2+H$	-776.888	518.693	0.561	0.6
GF	Null	921.515	0	1	0
Lichen	$WC+WC^2+H$	-820.122	515.067	0.599	0.575
Net min	Null	921.515	0	1	0
Nitrogen	$WC+WC^2$	-170.926	2886.259	0.779	0.815
SRR	$WC+WC^2+H$	-776.888	518.693	0.561	0.6
Timber	$WC+WC^2$	-378.595	951.22	0.779	0.839
Tree species	$WC+WC^2$	-378.595	951.22	0.779	0.839
PDI4					
AGB	$WC+WC^2+H$	-580.584	671.112	0.825	0.733
Carbon	$WC+WC^2+H$	-736.377	420.47	0.811	0.65
ECM	$WC+WC^2+H$	-580.584	671.112	0.825	0.733
GF	Null	921.515	0	1	0
Lichen	$WC+WC^2+H$	-580.584	671.112	0.825	0.733
Net min	Null	921.515	0	1	0
Nitrogen	$WC+WC^2$	-170.926	2886.259	0.779	0.815
SRR	$WC+WC^2+H$	-580.584	671.112	0.825	0.733
Timber	$WC+WC^2$	-378.595	951.22	0.779	0.839
Tree species	$WC+WC^2$	-378.595	951.22	0.779	0.839
PDI0					
AGB	Null	921.515	0	1	0
Carbon	Null	921.515	0	1	0
ECM	Null	921.515	0	1	0
GF	$WC+WC^2$	-378.595	951.22	0.779	0.839
Lichen	Null	921.515	0	1	0
Net min	$WC+WC^2$	-378.595	951.22	0.779	0.839
Nitrogen	$WC+WC^2$	-55.468	2658.102	0.779	0.935
SRR	Null	921.515	0	1	0
Timber	Null	921.515	0	1	0
Tree species	$WC*H+WC^2$	-964.985	1292.089	0.999	0.421

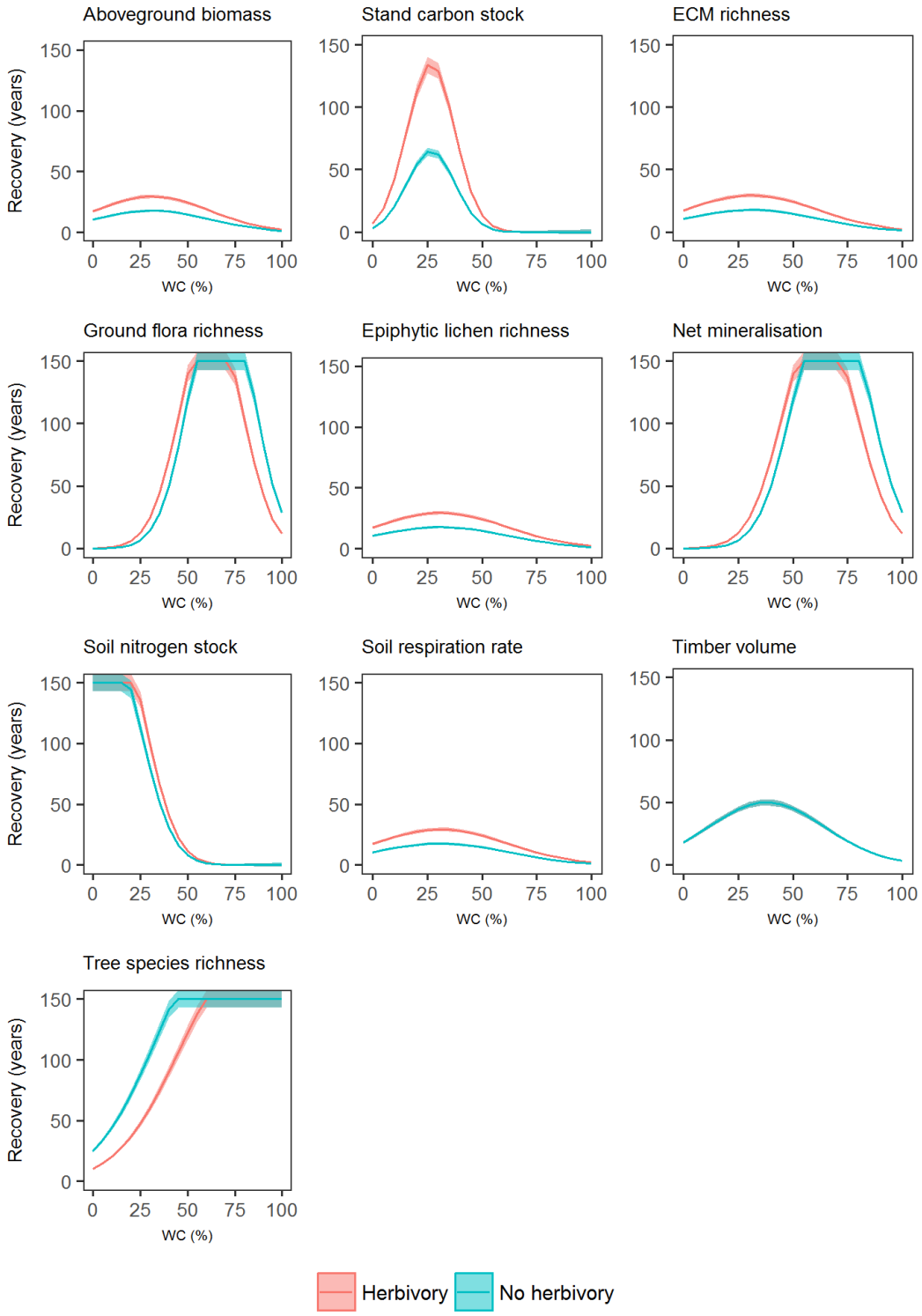

Fig. 5.11. Results of the most parsimonious GLMs for recovery time of the different ecosystem properties across the woodland cover (WC) gradient resulting from PDI1. The red and blue lines and surrounds represent the most parsimonious model, with and without herbivory, respectively. The coloured surrounds represent the 95% confidence intervals of the most parsimonious model. Note: where herbivory did not have a significant effect in the most parsimonious model both lines and confidence intervals overlap, with the only the blue lines and surrounds showing.

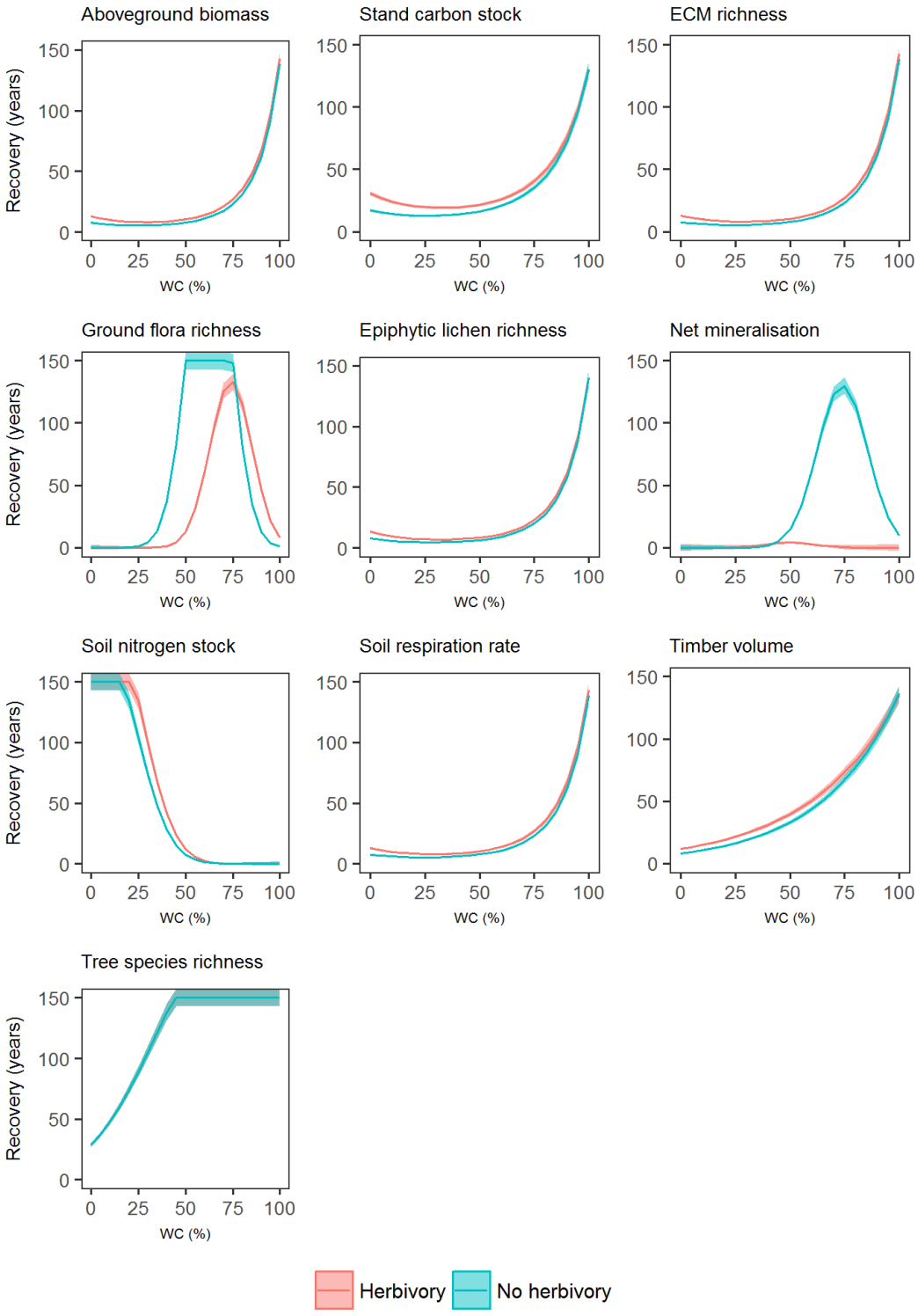

Fig. 5.12. Results of the most parsimonious GLMs for recovery time of the different ecosystem properties across the woodland cover (WC) gradient resulting from PDI2. The red and blue lines and surrounds represent the most parsimonious model, with and without herbivory, respectively. The coloured surrounds represent the 95% confidence intervals of the most parsimonious model. Note: where herbivory did not have a significant effect in the most parsimonious model both lines and confidence intervals overlap, with the only the blue lines and surrounds showing.

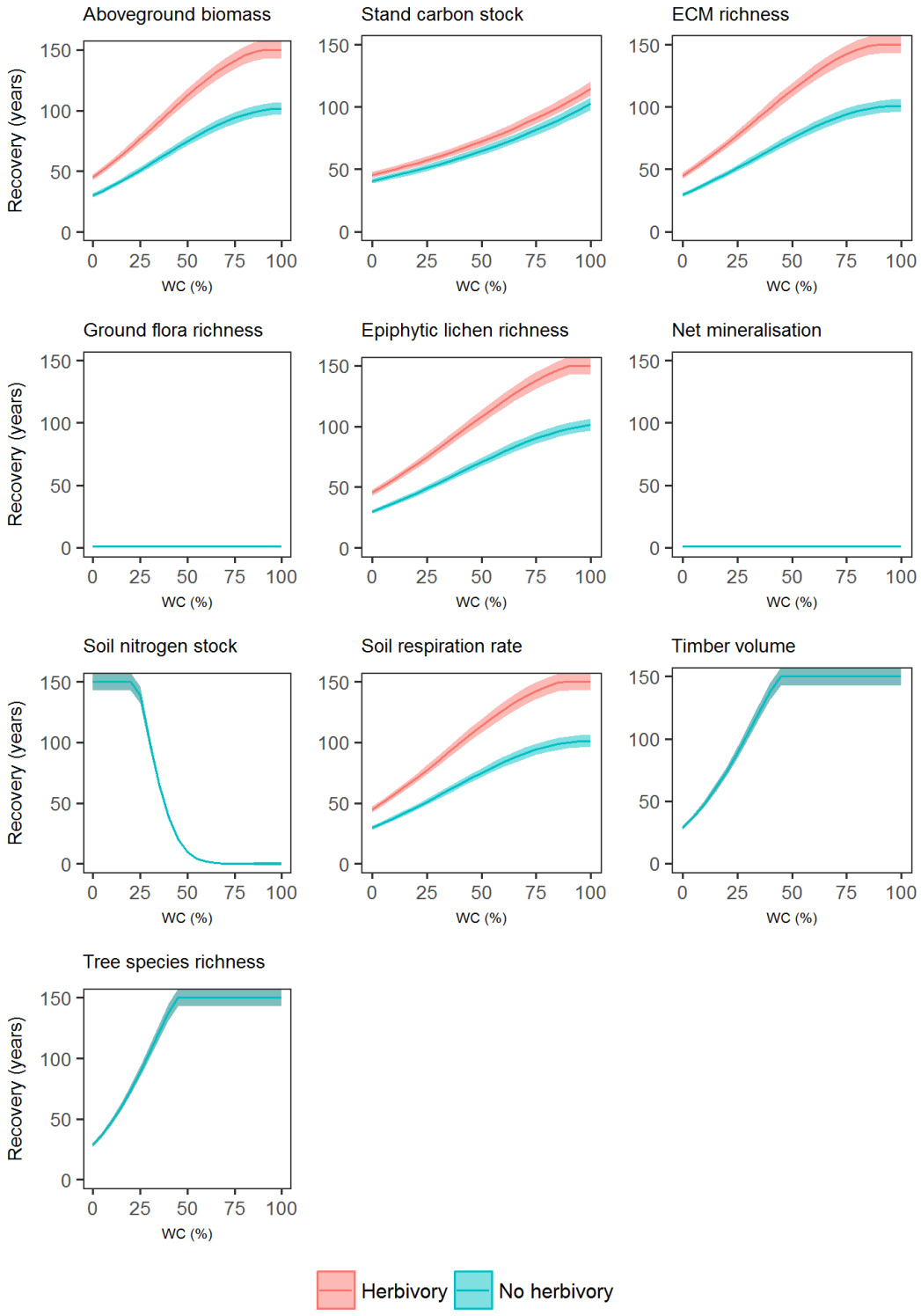

Fig. 5.13. Results of the most parsimonious GLMs for recovery time of the different ecosystem properties across the woodland cover (WC) gradient resulting from PDI3. The red and blue lines and surrounds represent the most parsimonious model, with and without herbivory, respectively. The coloured surrounds represent the 95% confidence intervals of the most parsimonious model. Note: where herbivory did not have a significant effect in the most parsimonious model both lines and confidence intervals overlap, with the only the blue lines and surrounds showing.

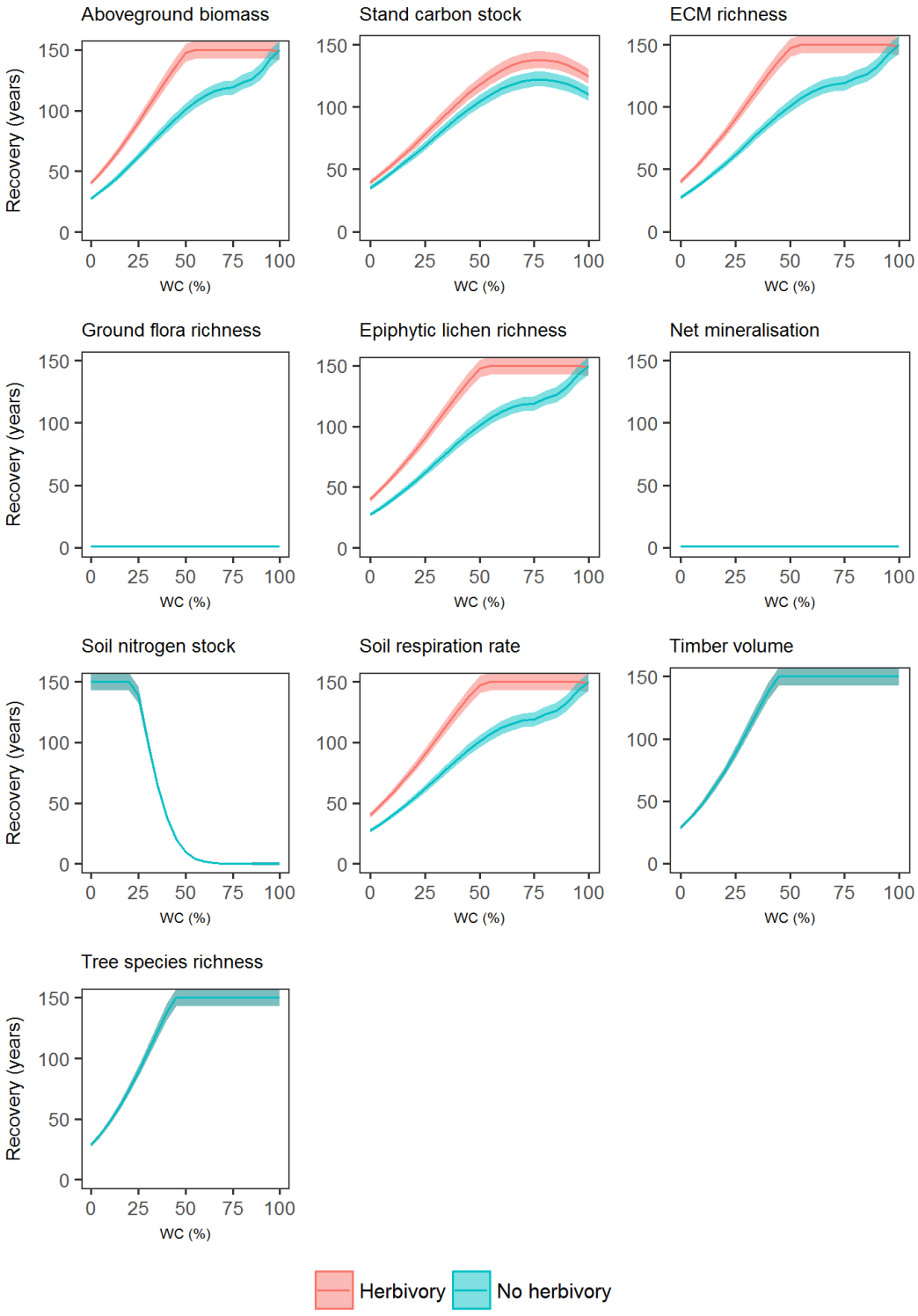

Fig. 5.14. Results of the most parsimonious GLMs for recovery time of the different ecosystem properties across the woodland cover (WC) gradient resulting from PDI4. The red and blue lines and surrounds represent the most parsimonious model, with and without herbivory, respectively. The coloured surrounds represent the 95% confidence intervals of the most parsimonious model. Note: where herbivory did not have a significant effect in the most parsimonious model both lines and confidence intervals overlap, with the only the blue lines and surrounds showing.

Table 5.5: Summary table of the influence of woodland cover (WC) on the individual resilience attributes. PDI indicates the pulse disturbance intensity that the resilience attribute was measured in response to. The number in each column relates to how many EPs included those terms in the most parsimonious models. The 'No WC relationship' column indicates the numbers of times the most parsimonious model did not include a WC term, or where ΔAIC < 4 compared to the null model, in accordance with the *a priori* criteria. The Total rows are the sum of the of the four PDI that included a pulse disturbance (i.e. not PDI0), and these numbers are out of 40, which relates to the EPs multiplied by the number of PDI scenarios that involved a pulse disturbance. H and WC*H indicate whether there was a significant effect of herbivory or a significant interaction between H and WC, respectively.

Resilience attribute	PDI scenario	No WC relationship	WC (linear)	WC (Non-linear)	Total WC models for each PDI	H	WC*H
Resistance	PDI1	7	2	1	3	NA	NA
	PDI2	5	4	1	5	NA	NA
	PDI3	5	3	2	5	NA	NA
	PDI4	5	3	2	5	NA	NA
	Total	**22**	**12**	**6**	**18**	**NA**	**NA**
	PDI0	6	2	2	4	NA	NA
Persistence	PDI1	6	1	3	4	2	0
	PDI2	4	0	6	6	2	0
	PDI3	4	4	2	6	5	0
	PDI4	7	1	2	3	3	0
	Total	**21**	**6**	**13**	**19**	**12**	**0**
	PDI0	6	4	0	4	1	0
Recovery	PDI1	0	0	10	10	5	4
	PDI2	0	1	9	10	0	9
	PDI3	2	1	7	8	5	0
	PDI4	2	0	8	8	5	0
	Total	**4**	**2**	**34**	**36**	**15**	**13**
	PDI0	6	0	4	4	0	1

5.4.6. Relationships between the three resilient attributes

Generally, all three resilient attributes (resistance, persistence and recovery) were highly correlated for each PDI scenario where correlations could be calculated (Table 5.6). Under the PDI1 scenario, when correlations could be calculated, seven out of eight EPs demonstrated negative correlations between resistance and recovery time, five out of five EPs demonstrated negative correlations between persistence and recovery time, and three out of three demonstrated positive correlations between resistance and persistence. Under the PDI2 scenario, the persistence of all EPs correlated negatively with recovery time, as did resistance for the eight times it could be calculated. Correlations were all positive between persistence and resistance for the eight relationships that could be calculated. Correlations were the same for PDI3 and PDI4: 100% (of the eight EPs correlations that could calculated) demonstrated significantly negative correlations between persistence and recovery time and between resistance and recovery time, and positive correlations between persistence and resistance. Overall, nitrogen stock had the strongest set of correlations among the three resilient attributes, exhibiting consistent, coherent relationships regardless of the PDI scenario, while the resilient attributes of carbon storage and timber volume had the strongest relationships in scenarios PDI2-4. The results were similar when each PDI scenario was subset into simulations with additional herbivory (press) disturbance and those without. However, there were two, three, one and three fewer significant relationships when herbivory was present compared to when there was no herbivory for PDI1, PDI2, PDI3 and PDI4, respectively (CD, CD5.4).

5.5. Discussion

The concept of resilience is being increasingly used in landscape management plans in efforts to enhance the future conservation of biodiversity and sustainability of ES (Biggs et al. 2012; Turner et al. 2012; Newton and Cantarello, 2015; Seidl et al. 2016). However, this is inhibited by broad assumptions about what makes a landscape resilient and that there are often no quantifiable metrics to determine resilience (Newton, 2016). To elucidate what effect WC, an often-used proxy for connectivity, had on landscape resilience, this original study measured resilience in the quantifiable and operational forms of resistance, persistence and recovery for important woodland EPs. The main findings showed that the initial WC of a landscape influenced resilience for over half of the EPs studied, with 72 out of 120 GLMs including WC as a significant term in the most parsimonious model. Specifically, WC had an effect on resistance, persistence and recovery time of 18, 18 and 36 EPs out of 40, respectively, when the results from the four

PDI scenarios that involved pulse disturbances were combined. Overall, the results provide support for the hypothesis of this study, that the initial WC of a landscape influences the resilience of a landscape, meaning connectivity is an important factor of landscape resilience (Fahrig, 2013; Tambosi et al. 2014). This is encouraging for conservation, as using increasing habitat cover as a way of promoting connectivity is gaining more focus as a way of making natural systems more resilient to future pressures (e.g. MEA, 2005; Watts et al. 2005; Lawton et al. 2010; Gimona et al. 2012; Mitchell et al. 2013).

5.5.1. Resilience of 0% woodland cover

One clear yet major unexpected finding of this study was that the 0% WC stage was consistently the most resilient – at 0% WC all three resilient attributes rarely changed from the 'most resilient' levels (i.e. immediate recovery and the highest persistence and resistance) (Fig. 5.3 – 5.14; Appendix 5.2 and Appendix 5.7). However, this result has to be interpreted with caution, as comparing a 0% WC landscape (i.e. one with no wooded areas, instead consisting of only heathland and grassland) with wooded ones, in some ways may be a false analogy, leading to erroneous interpretation. In reality, 0% WC could only exist on a previously-wooded landscape after undergoing deforestation brought about by anthropogenic or natural causes. In such circumstances, the whole landscape would have entered an alternate stable state (Lewontin, 1969), resulting in distinct configurations under the same set of environmental conditions (Scheffer and Carpenter, 2003). As resilience depends on the initial change that an EP experiences as the results of a disturbance, woodland-associated EPs are highly resistant at 0% WC because they had less to lose from disturbance. For instance, at 0% forest cover, fruit biomass has also been found to be low (Pessoa et al. 2017). Therefore, such landscapes should to be viewed differently from those that lost greater amounts (Nimmo et al. 2015). Thus, while a landscape of 0% WC may be very resilient, as shown here, it may be in a different way to other stages with greater WC (Standish et al. 2014). Additionally, as pointed out by Suding and Hobbs (2009), landscapes with very low habitat cover and connectivity would require much greater action to be useful for providing habitat for biodiversity or ES. Therefore, resilience of such landscapes may be irrelevant.

The results of a highly resilient 0% WC stage also meant that most GLM trends began with declines in persistence and resistance and increases in recovery time as WC went from 0% to 25%. This likely also acted to skew the results of the GLMs by providing highly influential points (Zuur et al. 2009). Therefore, for the above two reasons,

additional analyses using the same methods were conducted with 0% WC excluded. The additional results (herein referred to as Res25, with the original analysis referred to as Res0) can be found in Appendix 5.2, with the differences briefly described here. With 0% WC excluded, there was slightly more evidence of WC influencing landscape resilience as the number of most parsimonious models that featured some relationship with WC was two higher than in Res0, 75 compared with 72. The individual resilience attributes also differed in the number of times they were specifically affected by WC; for Res25 WC had an effect 24 times on resistance, 20 times on persistence and 31 times on recovery time, which was 18, 18 and 36 for the respective resilience attributes for Res0. Additionally, the shape of relationships between resilience and WC also differed with the number of non-linear WC relationships in the Res25 analysis being 69 compared to 53 from Res0. The Res25 most parsimonious models also generally had higher delta AIC and r^2_{adj} than their original alternatives, giving them more support. Lastly, without the influence of the 0% WC points, a lot of resilience relationships exhibited either downward-facing concave (resistance and persistence) or upward-facing concave (recovery time) relationships with WC, indicating that resilience was greater in the intermediate ranges of WC (50-75% WC). This was particularly true when landscapes were subjected to higher intensities of disturbance. Additionally, with 0% WC excluded, the number of significant correlations between resistance and recovery time was reduced under the PDI3 and PDI4 scenarios (Table A5.7).

5.5.2. Effect of disturbance intensity

Pulse disturbances cause large-scale tree mortality in forests worldwide, reducing the amount of biomass of living vegetation (Dale et al. 2001; Anderegg et al. 2013; Treu et al. 2014; Allen et al. 2015). In this study, the percentage reduction of landscape AGB differed greatly as a result of both the PDI scenario and the initial WC. For PDI1 and PDI2 scenarios, only oak and only beech were eliminated, respectively. A comparison of the resistance results from these two scenarios highlighted that the species affected is important to the overall resilience of the forest – at 25% WC, the effect of removing oak was greater than that of removing beech, while for other WCs > 25%, the opposite was true. In this way, resistance depended on the abundance of a species susceptible to disturbance. Similar was concluded by Tanner and Bellingham (2006) who found that forests with abundant species that were less susceptible to structural damage and subsequent mortality had greater resistance to hurricanes, with resistance being measured in terms of turnover of trees in that study. Moreover, resistance to species-specific pest

and pathogen attacks is low in forests with a high abundance of vulnerable species (Treu et al. 2014), and the reason why host species abundance is used as one of the main parameters in modelling pest and pathogen spread (Meentemeyer et al. 2004; Cunniffe et al. 2016). Thus, the effect of disturbance is mediated by the relative composition of the initial WC rather than total WC amount, owing to some species being much less affected by disturbance (Tanner and Bellingham, 2006; Pretzsch et al. 2013). In contrast, Grossiord et al. (2014) found disturbance was more intense and resistance lower in forests with mixed species. While that study focused on a less species-specific disturbance of drought, it highlighted that abundance of a single species may make a forest more resilient if that means that dominance excludes highly competitive pioneer species, which in that study was birch, a species that has high water consumption. Such phenomena could affect the resilience of forests more as the climate changes (Malhi et al. 2008; Moritz and Agudo, 2013).

5.5.3. Non-linear relationships between WC and resilience

When 0% WC is ignored, AGB and EPs whose values were calculated based on AGB, namely ECM richness, SRR and lichen richness, were most resilient in the intermediate stages (Appendix 5.4). This could possibly be attributed to a single species accounting for approximately 46% of pre-disturbance AGB for the 25% and 100% WC stages, which were oak and beech, respectively (Appendix 5.5). The 50% and 75% WC stages – the more resilient stages – had no particular dominance. Thus, in the context of this study, the 25% and 100% stages acted as more homogenised landscapes, in terms of the proportion of overall AGB. Consequently, owing to the pulse disturbances being species specific, disproportionately more damage was done to landscapes with high dominance of a single species, resulting in a higher proportion of AGB being removed (Table A5.7; Fig. 5.2).

The results provide support for a theory that intermediate amounts of habitat cover provide optimal resilience (Biggs et al. 2012; Grêt-Regamey et al. 2014; Altieri et al. 2015), which is similarly often attributed to the domination of landscapes by a single species. Such landscapes increase the opportunities of movement or dispersal of an EP, but also opportunities of disturbances (e.g. pathogens, invasive species and abiotic conditions) to be propagated due to ecological conditions remaining constant (Loreau et al. 2003; Rahel, 2007; Gonzalez et al. 2009; Schippers et al. 2014). For instance, the results of a meta-analysis that compared the incidence of insect herbivory on the same species in singles-species and mixed-species forests showed that herbivory was

significantly more prevalent in the monoculture stands (Jactel and Brockerhoff, 2010). Thus, the results and mechanistic hypotheses match findings that state mixed-species stands are needed for greater resilience of forests in the future (Lindner et al. 2010; Parks and Bernier, 2010), which are ultimately sustained through woodland expansion. Therefore, the chance of expansion of woodland may increase its resilience.

Another reason that 100% WC was often less resilient than lower WC stages may be due to the initial tree species richness being a third lower in 100% WC than in either 50% or 75% WC (CD, CD 5.11). This likely reduced the availability of potential seed sources, owing partly to increased distances from remaining species, and therefore the stand replacing rate. This was found by Morin et al. (2011) who ran simulation models with disturbances and different initial numbers of temperate tree species. The authors concluded that more rapid responses and recovery of productivity to mortality events occurred when species diversity was higher. They attributed the results to the shading regimes and shade tolerances of the different species, whereby the different species with diverse functional responses to light were able to exploit the available light better. This is similar to the results of this study where the rate of succession and expansion seem to be reduced in the 100% WC stages following disturbance compared to the lower WC stages. Through the process of succession across an undisturbed landscape, which was simulated to create the 100% WC, stands became eventually dominated by shade-tolerant species, which resulted in tree species richness declining over time.

Carbon stock, a combination of C in soil and vegetation, generally followed the trajectory of AGB for all three resilience attributes, even though its calculation was not derived directly from AGB. As carbon storage in forests depends largely on carbon assimilation and translocation, initiated mostly through photosynthesis (Chen et al. 2014), harvesting AGB can reduce C stock in forests by 60% initially (Keith et al. 2014). This also reduces the chance of assimilation of carbon (Chen et al. 2014). Thus, AGB still plays the main role in carbon storage for forests, explaining the similar relationships recorded.

5.5.4. Other relationships between WC and resilience

Resilience was not always most favourable in the intermediate WC stages; the resilience of some EPs showed the opposite trend or no change (GF and net mineralisation), some were dependent mostly on the PDI (timber volume), some did not change much (e.g. nitrogen stock), and tree species richness was observed to change even in the PDI0 scenario, reflecting a natural dynamic presumed to affect all landscapes irrespective of

whether they were subject to a pulse disturbance or not. The empirical relationships measured in Chapter 2 between AGB loss and GF and net mineralisation were positive, meaning that they increased when AGB declined. Due to these relationships, which have been observed when comparing woodland to grassland (i.e. 0% WC) (Booth et al. 2005; Zenner et al. 2006), decreases in tree AGB caused by disturbance allowed both GF and net mineralisation to increase. As all resilience measures were based on the pre-disturbance value of EPs, this meant that GF and net mineralisation were always resistant to disturbances that impact trees, which fits with the results of this study. However, the persistence and recovery time of these two EPs did change depending on the initial WC when the pulse disturbance had lower intensity (i.e. PDI1 and PDI2) – they displayed non-linear relationships, with intermediate WC being the least favourable for resilience. As the quantity of eliminated AGB was low (< 20%; Table A5.7) for the combination of these PDI scenarios and initial intermediate WC, recovery of AGB due to succession and woodland expansion occurred between 60 and 100 years (CD, CD5.11). This meant that GF never recovered in these instances, although, due to the slightly less steep relationship with AGB (Chapter 2), net mineralisation did for PDI2 when herbivory was present.

The disparate results of the individual EPs here indicate that there is a possible danger of relying wholly on resilience and not considering the intrinsic value of the individual EPs, especially when considering it in an ecological context for determining future actions (Standish et al. 2014; Newton, 2016). Thus, EPs are often important to be assessed separately (Carpenter, 2001) because if other EPs were of interest, values may be quite different. For example, a study in the New Forest found that biodiversity value of species of conservation concern were higher in heathlands than in the woodlands (Cordingley et al. 2015); however, that study did not include specific woodland associated biodiversity, such as ECM or lichen.

5.5.5. Effect of herbivory

Herbivory, the press disturbance in this study, often exacerbated the impact of the pulse disturbance, frequently having an influential effect on resilience. Herbivory was a significant factor in persistence and recovery for just under half of the assessed EPs when the pulse disturbance involved the removal of more than one species (Table 5.5). This caused some EPs, especially those related directly to AGB, to never recover compared to the same scenarios when herbivory was not simulated (CD, CD5.11). This is likely explained due to herbivory being one of the main factors limiting recruitment of new trees (Bergmeier et al. 2010; Churski et al. 2017), the continued effect of disturbance impacting

regeneration and regrowth (Rydgren et al. 2004; Tarvainen et al. 2015; Cantarello et al. *in press*). However, a study by Newton et al. (2013) found that regeneration occurred even when the area was heavily browsed by herbivores. Newton and colleagues examined the effects of herbivory on regeneration of tree species and woodland expansion in the New Forest using the LANDIS-II model, which was validated by field-collected regeneration data. This study found similar results but only in simulations when there was no pulse disturbance (i.e. PDI0), a factor which was also not present in the study of Newton et al. (2013). Therefore, the difference in the effect of herbivory is likely to arise from the presence of the major prior pulse disturbance. Since regeneration normally occurs following a pulse disturbance due to the creation of canopy gaps that alleviates competition for light, nutrients and water (McCarthy, 2001; Carvalho et al. 2004; Peña-Claros et al. 2008), seedling and sapling abundance is much greater in canopy gaps than under closed forest (Camisón et al. 2015; Sharma et al. 2016). The regrowth of the forest, which is essential for overall persistence and recovery, relies on the abundance of such seedlings reaching maturity following a pulse disturbance, as evidenced by the counterpart scenarios in which herbivory was not simulated. Consequently, the presence of herbivory had a great impact, slowing regrowth substantially, a phenomenon that is already being observed in the New Forest after large-scale dieback deriving from a like pulse disturbance of drought (Martin et al. 2015).

5.5.6. Interpretation of results

Like all ecological models, there are a number of limitations to do with the models used in this study, which can lead to uncertainty; therefore, the results should be interpreted with the acknowledged uncertainties. One of the key issues in reducing uncertainty is validation of the model outputs. While no model validation was carried out specifically for this Chapter, previous work that used a very similar version of the model in the same location has been undertaken, providing a high level of accuracy. This is explained further in section 6.3.6. Additionally, sensitivity analyses could have helped in the interpretation of the results presented here. As discussed in Cariboni et al. (2006), sensitivity analyses help to quantify how a change in a single parameter affects the overall results, and thus how much influence a slight change in the value of one input may have on the overall results. Sensitivity analyses help to provide further evidence of the robustness of a model, determing how uncertain the results may be, e.g. for those where sensitivity is not demonstrated, greater confidence can be placed in the overall conclusions and therefore in any management or policy recommendations based on them. In this study, sensitivity

analyses could have been performed on a number of the LANDIS-II inputs, such as the level of herbivory or certain life history attributes. Resulting from sensitivity analyses on the life history attributes in LANDIS-II, Simons-Legaard et al. (2015) showed that two of the most sensitive parameters were the maximum allowable AGB and the duration the model was run for. Therefore, running sensitivity analyses after altering those attributes one at a time could have helped to determine how certain the model was in its projections. This should be considered carefully when interpreting the results of this study, or any ecological study that utilises mathematical models (Simons-Legaard et al. 2015).

5.6. Conclusions

The prospect of rapid woodland loss might seem far-fetched currently, owing to global drivers such as pathogens currently only having a relatively small impact in temperate woodlands. However, large-scale attacks are increasing in temperate forests in Europe (Kowalski, 2006; La Porta et al. 2008; Jung et al. 2009; Santini et al. 2013) and elsewhere (Flower and Gonzalez-Meler, 2015). In order to be able to protect forests for important EPs, actions taken presently will help to define how resilient wooded landscapes are. On the basis of the results in this study, it is clear that WC has an influence on the resilience of most EPs, with EPs generally having better resistance, persistence and recovery time when WC is 50%-75%. This is likely owing largely to those landscapes being more resistant to the initial pulse disturbances as there is less dominance of a single species that can be affected by the species-specific disturbance. Moreover, the 100% WC generally had worse resilience due to not being able to expand, a process that needs to be considered in future management plans. Herbivory is also likely to have a greater impact on the persistence and recovery time of most EPs subsequent to a pulse disturbance, something which is already being observed in the New Forest. Therefore, any policy seeking to improve landscape resilience should aim to improve the woodland connectivity to an extent where WC is > 50% and has high tree species richness but that leaves room for natural woodland expansion. Also, other disturbances need to be considered as they may have a greater impact subsequent to a pulse disturbance.

Table 5.6: Results of Spearman Rank correlations between the different resilience attributes (RAs), persistence (per), resistance (res) and recovery (rec), for all the ecosystem properties under the different pulse disturbance intensity (PDI) scenarios. Values shown in bold are considered are significant to the alpha level of 0.005. *r* represents the Spearman's correlation coefficients and r^2 represents the variation explained. A '-' represents correlations that could not be calculated due at least one attribute of resilience not changing across the woodland cover gradient.

Ecosystem property	RAs tested	PDI1			PDI2			PDI3			PDI4			PDI0		
		r	*p*	r^2	*r*	*p*	r^2	*r*	*p*	r^2	*r*	*p*	r^2	*r*	*p*	r^2
AGB	per-rec	-	-	-	-0.71	< 0.001	**0.504**	-0.862	< 0.001	**0.743**	-0.872	< 0.001	**0.76**	-	-	-
	per-res	-	-	-	0.695	< 0.001	**0.483**	0.612	< 0.001	**0.375**	0.754	< 0.001	**0.569**	-	-	-
	res-rec	-0.487	0.006	0.237	-0.922	< 0.001	**0.85**	-0.765	< 0.001	**0.585**	-0.715	< 0.001	**0.511**	-	-	-
ECM	per-rec	-	-	-	-0.71	< 0.001	**0.504**	-0.861	< 0.001	**0.741**	-0.854	< 0.001	**0.729**	-	-	-
	per-res	-	-	-	0.695	< 0.001	**0.483**	0.724	< 0.001	**0.524**	0.831	< 0.001	**0.691**	-	-	-
	res-rec	-0.861	< 0.001	**0.741**	-0.922	< 0.001	**0.85**	-0.765	< 0.001	**0.585**	-0.742	< 0.001	**0.551**	-	-	-
Lichen	per-rec	-	-	-	-0.723	< 0.001	**0.523**	-0.864	< 0.001	**0.746**	-0.872	< 0.001	**0.76**	-	-	-
	per-res	-	-	-	0.697	< 0.001	**0.486**	0.711	< 0.001	**0.506**	0.803	< 0.001	**0.645**	-	-	-
	res-rec	-0.842	< 0.001	**0.709**	-0.93	< 0.001	**0.865**	-0.755	< 0.001	**0.57**	-0.742	< 0.001	**0.551**	-	-	-
GF	per-rec	-0.769	< 0.001	**0.591**	-0.664	< 0.001	**0.441**	-	-	-	-	-	-	-0.696	< 0.001	**0.484**
	per-res	-	-	-	-	-	-	-	-	-	-	-	-	0.782	< 0.001	**0.612**
	res-rec	-	-	-	-	-	-	-	-	-	-	-	-	-0.696	< 0.001	**0.484**
Net min	per-rec	-0.628	< 0.001	**0.394**	-0.537	0.002	**0.288**	-	-	-	-	-	-	-0.696	< 0.001	**0.484**
	per-res	-	-	-	-	-	-	-	-	-	-	-	-	0.754	< 0.001	**0.569**
	res-rec	-	-	-	-	-	-	-	-	-	-	-	-	-0.696	< 0.001	**0.484**
Nitrogen	per-rec	-0.894	< 0.001	**0.799**	-0.894	< 0.001	**0.799**	-0.959	< 0.001	**0.92**	-0.959	< 0.001	**0.92**	-0.992	< 0.001	**0.984**
	per-res	0.775	< 0.001	**0.601**	0.909	< 0.001	**0.826**	0.776	< 0.001	**0.602**	0.568	0.001	**0.323**	0.994	< 0.001	**0.988**
	res-rec	-0.951	< 0.001	**0.904**	-0.982	< 0.001	**0.964**	-0.853	< 0.001	**0.728**	-0.566	0.001	**0.32**	-0.992	< 0.001	**0.984**
SRR	per-rec	-	-	-	-0.71	< 0.001	**0.504**	-0.861	< 0.001	**0.741**	-0.854	< 0.001	**0.729**	-	-	-
	per-res	-	-	-	0.695	< 0.001	**0.483**	0.749	< 0.001	**0.561**	0.847	< 0.001	**0.717**	-	-	-
	res-rec	-0.861	< 0.001	**0.741**	-0.922	< 0.001	**0.85**	-0.817	< 0.001	**0.667**	-0.742	< 0.001	**0.551**	-	-	-
Carbon	per-rec	-0.744	< 0.001	**0.554**	-0.717	< 0.001	**0.514**	-0.878	< 0.001	**0.771**	-0.885	< 0.001	**0.783**	-	-	-
	per-res	0.522	0.003	**0.272**	0.689	< 0.001	**0.475**	0.799	< 0.001	**0.638**	0.827	< 0.001	**0.684**	-	-	-
	res-rec	-0.7	< 0.001	**0.49**	-0.95	< 0.001	**0.902**	-0.941	< 0.001	**0.885**	-0.792	< 0.001	**0.627**	-	-	-
Timber	per-rec	-	-	-	-0.717	< 0.001	**0.514**	-0.86	< 0.001	**0.74**	-1	< 0.001	**1**	-	-	-
	per-res	-	-	-	0.695	< 0.001	**0.483**	0.9	< 0.001	**0.81**	1	< 0.001	**1**	-	-	-
	res-rec	-0.946	< 0.001	**0.895**	-0.9	< 0.001	**0.81**	-0.86	< 0.001	**0.74**	-1	< 0.001	**1**	-	-	-
Tree species	per-rec	-0.77	< 0.001	**0.593**	-0.696	< 0.001	**0.484**	-0.696	< 0.001	**0.484**	-0.696	< 0.001	**0.484**	-0.853	< 0.001	**0.728**
	per-res	0.696	< 0.001	**0.484**	0.647	< 0.001	**0.419**	0.675	< 0.001	**0.456**	0.695	< 0.001	**0.483**	0.762	< 0.001	**0.581**
	res-rec	-0.59	0.001	**0.348**	-0.697	< 0.001	**0.486**	-0.699	< 0.001	**0.489**	-0.697	< 0.001	**0.486**	-0.959	< 0.001	**0.92**

Chapter 6:
Discussion

6.1. Original contribution to knowledge

The findings in this thesis make original contributions to different scientific topics, particularly the fields of ecology, ecological indicators, and resilience. Original contributions to ecology include insight into the trajectories of important ecological aspects of a temperate woodland, such as biodiversity and ecosystem functions, as woodland degrades. This highlighted the dynamic changes of ecosystem properties that occur. Through testing many ecological indicators and condition assessments over condition gradients, new knowledge has been obtained that emphasises which indicators are appropriate to include in future condition assessments and which are insufficient. Such knowledge also contributes to the understanding of protected area assessment and management, including the current inadequacies of CSM, the current statutory assessment tool for SSSIs in the UK, which had never been empirically examined before. Most notably, all the findings in this thesis contribute novel knowledge that enhances overall understanding of resilience and its related concepts. Specifically, new and important knowledge relating to ecological thresholds was elucidated, together with information about what makes a landscape resilient and whether resilience can be monitored and assessed through surrogate measures. All the novel results presented in this thesis can also be used by managers of temperate landscapes, to contribute to future conservation management plans.

6.2. Summary of the main findings

The results in this thesis have identified how underlying ecosystem properties (EPs) of woodlands, which include biodiversity and ecosystem functions, change with increasing intensity of environment disturbance, both at the stand and landscape scale. Moreover, the effectiveness of rapid condition assessment tools was tested to determine whether they were sensitive to changes in woodland condition. The combined results of all the chapters could then be used to examine whether the rapid assessment tools could also be used to accurately assess resilience. For a summary of hypotheses tested and support for them, see Table 6.1.

In Chapter 2, the issue of ecological thresholds was tested for an ecosystem that was undergoing large-scale dieback. Ecological thresholds are defined as points where relatively rapid change occurs in the state of any ecosystem variable (Huggett et al. 2005;

Allen et al. 2016) and are of major scientific and societal interest and debate (Barnosky et al. 2012; Brook et al. 2013). Prior to this thesis, knowledge regarding the issue of thresholds occurring in natural systems was largely theoretical, especially for terrestrial ecosystems (Scheffer et al. 2001; Dakos et al. 2008). As hypothesised, the results of Chapter 2 confirmed theoretical predictions that thresholds were found to exist in the different EPs across a gradient of degradation. Most noticeably, thresholds were observed in some of the biodiversity aspects measured; distinct thresholds were exhibited at different stages along the dieback gradient for ectomycorrhizal fungi (ECM), epiphytic lichen and vascular ground flora richness. ECM and lichen richness showed declines after thresholds were exceeded before 50% dieback had occurred, while ground flora richness showed a threshold towards the end of the dieback gradient, causing ground flora richness to increase less sharply > 75% dieback compared to that of the rest of the dieback gradient. There was only a single ecosystem function that exhibited a threshold, the soil respiration rate, which declined initially and then plateaued after approximately 50% dieback. Moreover, numerous ecosystem conditions, including sward height, palatable seedling abundance and understorey biomass were among the variables that exhibited threshold responses. No other studies, as far as is known, have examined threshold responses over a gradient of stand dieback. However, other research has shown that threshold responses exist in response to human-derived habitat loss and degradation (Fahrig, 2002; Bodin et al. 2006; De Filho and Metzger, 2006; Ochoa-Quintero et al. 2015; Rocha-Santos et al. 2016). The underlying mechanisms thought to be responsible for causing ecological thresholds are switches from negative feedbacks to positive feedbacks. While one such mechanism is predicted in the Discussion of Chapter 2, specifically relating to the ECM threshold, feedbacks is one area of interest that needs a lot of further research.

In Chapter 5, a test of the hypothesis that initial woodland cover (WC), as a proxy of connectivity, influences landscape resilience under different disturbance intensities was tested. There had been very little research on the effect of connectivity on resilience prior to this thesis, even though increasing connectivity is perceived as a way of increasing terrestrial landscape resilience (Heller and Zavaleta, 2009; Lawton et al. 2010; Oliver et al. 2015). Previously, evidence of connectivity relating to resilience had mostly been obtained from aquatic systems, notably coral reefs (Mumby and Hastings, 2008; Adam et al. 2011; Vergés et al. 2011; Olds et al. 2012). In terrestrial ecosystems, connectivity studies have mainly focused on persistence of biodiversity (e.g. Fahrig, 2013; Tambosi et al. 2014; Herrault et al. 2016), and have not included other important ecosystem properties, including ES (Mitchell et al. 2013). Moreover, very few landscape

connectivity studies have included the different attributes of resilience (i.e. resistance, persistence and recovery), giving an incomplete description of overall resilience. Here, the results suggest that the habitat area of WC is highly influential for all aspects of resilience for several EPs assessed over the different scenarios of pulse disturbance intensity. This was most noticeably the case for the recovery time, which often resulted in a non-linear relationship with WC. The findings generally agree with other studies that theorise that connectivity is an important factor for resilience (Fahrig, 2013; Tambosi et al. 2014). Furthermore, the results suggest that intermediate amounts of habitat cover, rather than high amounts of habitat cover, may provide optimal resilience, fitting with the hypotheses of others (Grêt-Regamey et al. 2014; Altieri et al. 2015). Nonetheless, some authors argue that it is not habitat amount that is important for persistence of some EPs, but other determinates of connectivity: spatial configuration and isolation of habitats (Mitchell et al. 2014; Haddad et al. 2017). Thus, more aspects of connectivity should be considered in future research.

To answer the main question of how resilient the temperate woodlands of the New Forest are, the results in Chapter 5, which were based on empirical values from Chapter 2, suggest that with its current WC, which is approximately 46% (JNCC, 2011), the New Forest has quite high resilience. This is based on the finding that landscapes with 50% WC generally had high resilience for most EPs, regardless of disturbance. However, the results are not that definitive since over a third of the WC is coniferous woodland (JNCC, 2011), which was not assessed in Chapter 5. Consequently, the resilience of the New Forest to a pulse disturbance would depend on how similarly or disparately the two types of woodland responded.

Coniferous woodland resilience may be similar to that of broadleaved woodland in terms of non-biodiversity EPs. For instance, carbon storage in forest stands of the two phylogenetic groups can be similar, albeit highly variable (Thompson and Matthews, 1989; Scheller et al. 2012; Cook et al. 2014), meaning that stand-destroying disturbances could affect both types equally in terms of resistance. In contrast, major differences exist between the two woodland types for most biodiversity EPs, with broadleaved woodland generally having higher species richness than coniferous woodland (Fahy and Gormally, 1998; Fuller et al. 2008; Sweeney et al. 2010). Therefore, attributes of resilience for these EPs would likely be inferior for broadleaved woodlands, partially because there is a greater amount to lose initially, making total recovery less likely (Nimmo et al. 2015). However, measured in absolute terms, broadleaved woodlands may still house more species than coniferous woodland after disturbance (Fuller et al. 2008; Sweeney et al.

2010). In terms of landscape resilience, there are advantages of having a mix of coniferous and broadleaved woodlands, which could enhance overall resilience. Mixed landscapes generally have greater species diversity. Mixed species landscapes often increase the initial provision of different EPs (Gamfeldt et al. 2013; Turner et al. 2013; Schuler et al. 2016), the amount of suitable habitat area for certain woodland-associated species; and, more importantly for resilience, the functional responses to disturbance (Morin et al. 2011; Turner et al. 2013). In a single ecosystem type, functioning of the ecosystem can depend largely on a single species (Sasaki and Lauenroth, 2011). Therefore, if a disturbance greatly affects that species, its disproportionate loss can reduce ecosystem resilience substantially (Grman et al. 2010; Sasaki and Lauenroth, 2011).

In summary, based on the findings of Chapter 5 that suggested WC influenced resilience at the landscape scale, the New Forest could be perceived as having good resistance, persistence and recovery time for most of its EPs studied, as its WC was just under 50%. However, the actual landscape is composed of a mixture of both broadleaved and coniferous woodland, the latter of which was not included in Chapter 5's experimental design. Therefore, in reality the resilience of coniferous woodlands could have a positive or negative affect on the overall resilience, which would need to be considered in any management plans that aim to enhance resilience for the New Forest.

In Chapter 3, CSM, the current statutory condition assessment tool for SSSIs in the UK, was tested across a known degradation gradient (loss of BA, in this case) to determine its effectiveness for assessing woodland condition. BA loss through tree mortality is currently a key indicator of forest condition (e.g. van Mantgem et al. 2009; Cantarello and Newton, 2008), therefore strong relationships between the CSM results and the BA loss gradient were expected. Overall CSM condition scores, most of which were specific to the New Forest, showed that there was slight variation across the BA loss gradient, however only one showed any significant difference between the individual stages of BA decline (when the analysis was run with Bonferroni-corrected values, no lists showed any significant differences between the individual stages). Also, particularly important was the fact that there was not a consistent trend, either positive or negative, as might be expected when assessing condition against declining woodland area (i.e. BA). The findings imply that CSM is not an altogether effective tool to be used when assessing changing condition, as sensitivity to variation in condition is low. These results agree with others who found that such assessments were ineffective to determine condition (Gaston et al. 2006; Davies et al. 2007), possibly due to lack of specificity in targets (Davies et al. 2007; Jackson and Gaston, 2008; Lindenmayer et al. 2012). Nonetheless, other non-CSM

indicators were also recorded along the BA loss gradient, of which factors such as the richness of ECM and ground flora, canopy cover and some soil measures differed significantly, agreeing with other similar research (Neufeld and Young, 2014; Treu et al. 2014). However, while most individual indicators showed either positive or negative trends across the dieback gradient, the change was never consistent between each subsequent stage. Consequently, using a single indicator might have little effectiveness in detecting changing condition, but combinations of indicators, especially ones with opposing trends, may work effectively (Niemi and McDonald, 2004; Oliver et al. 2014; Gao et al. 2015; Lawley et al. 2016). A mixture of the current CSM targets and the non-CSM indicators that demonstrated change over the woodland condition gradient could be tested to determine the most suitable combination for effective assessment of woodland condition in the future.

In Chapter 4, the hypotheses all pertained to structural woodland condition measures obtained from airborne lidar being able to predict field-collected ecological habitat conditions measures. Specifically, field-collected metrics of biodiversity, stand condition, herbivore damage and soil condition were all tested against an array of lidar-derived structural variables. Of these, the biodiversity measures, particularly ground flora richness, showed the most substantial relationships with lidar-derived variables, indicating that there may be some utility in using lidar to predict the degradation level of woodlands. However, there was less evidence that this was true for herbivore damage and soil condition categories, which indicates that there are limitations to using lidar as a tool to infer overall condition and therefore current resilience.

In answer to the question of whether any tools can be used to infer the current resilience of woodlands in the New Forest, the results in Chapter 3 and Chapter 4 indicate that currently this would be difficult and ineffective. This is based on the idea of resilience assessments, which use surrogate measures, together with in-depth knowledge of a system (Bennett et al. 2005; Carpenter et al. 2005; Scheffer et al. 2015; Quinlan et al. 2016), to make inference about resilience. From the results in Chapter 2, the trajectories of many EPs in a forest undergoing dieback were known. These were important pre-cursors to resilience assessments (Scheffer et al. 2015). Therefore, any noteworthy findings from either of the current rapid, resource-efficient assessment tools tested in Chapter 3 (CSM condition assessments) or Chapter 4 (lidar) would have indicated that those tools were suitable for resilience assessments. Since some of the lidar-derived variables were found to be able to substantially predict ground flora richness, it could be determined that there is some utility in using lidar to predict the current resilience of

stands: the ground flora richness value inferred via a related lidar metric could subsequently be used to infer the stage of dieback in a stand, based on the results from Chapter 2. This would then allow inference of the value of other measured EPs also using Chapter 2's results. However, considering that lidar could not predict metrics of woodland condition that changed dramatically over the dieback gradient, such as ECM, this suggests that lidar may not be a sufficient tool to detect change other than in stand structure. More research needs to be carried out to explore whether this is accurate. In summary, combining results from both Chapters 3 and 4, it could be determined that at the current time the two tools tested were ineffective at detecting and therefore inferring resilience. This highlights the difficulty in choosing surrogate indicators when assessing condition let alone resilience, as a lot of variation exists in complex ecological systems (Carpenter et al. 2001; Filotas et al. 2014; Standish et al. 2014). Additionally, this indicates that there is an urgency to develop better tools to be able to assess changing condition of woodlands and therefore to be able to infer resilience.

Table 6.1: Summary table of the support for the hypotheses tested in this thesis.

Question: How resilient are the temperate woodlands of the New Forest and what tools can be used to infer resilience?			
	Hypotheses	Support for hypotheses	Relevance to main question
Chapter 2: Thresholds of biodiversity and ecosystem function in a forest ecosystem undergoing dieback (Objective 1)	Threshold responses exist in measures of: 1) biodiversity; 2) ecosystem function; and 3) ecosystem condition over a dieback gradient	1) Partially supported. For ectomycorrhizal fungi, epiphytic lichen and vascular ground flora richness, distinct thresholds were exhibited at different stages along the dieback gradient. However, other biodiversity showed linear responses (e.g. ground-dwelling arthropods). 2) Partially supported. A single ecosystem function showed a threshold response, namely soil respiration rate. 3) Partially supported. Sward height, palatable seedling abundance and understorey biomass were among ecosystem condition metrics to exhibit threshold responses.	The identification of thresholds is considered to be critical to exploring resilience in natural systems. The results of this chapter showed that thresholds do exist in certain ecosystem properties. Moreover, the results from this chapter showed the trajectory of all the EPs assessed over the dieback gradient. These values were used to determine resilience at the landscape scale (Chapter 5).
Chapter 3: The effectiveness of condition assessment for detecting change in woodland condition (Objective 2)	1) Common Standards Monitoring (CSM) condition assessment results will vary significantly over a gradient of environmentally-induced dieback. 2) Non-CSM indicators could be used to effectively determine different beech dieback	1) Partially supported. Significant differences were present across the gradient of dieback stages for the four CSM target lists used, based on ANOVAs. However, corrected pairwise comparisons between the dieback stages determined that only one of the CSM targets lists differed significantly between stages. 2) Partially supported. Indicators such as ectomycorrhizal fungi and ground flora richness, carbon storage and some soil measures significantly differ over the stages of environmentally-induced dieback.	The CSM guide for woodland is a commonly-used forest assessment tool for SSSIs, of which the New Forest is one. However, it did not effectively determine difference in condition. Therefore, the results here showed that CSM is not very effective when assessing woodland undergoing degradation and could not be used as a surrogate for resilience assessments. As some of the non-CSM indicators significantly differed over the dieback gradient, they could potentially be used as surrogates for resilience assessments, although more work is needed to confirm this.

Question: How resilient are the temperate woodlands of the New Forest and what tools can be used to infer resilience?			
	Hypotheses	Support for hypotheses	Relevance to main question
Chapter 4: Evaluation of the use of airborne lidar in detecting forest condition (Objective 2)	Field-measured variables of 1) biodiversity condition; 2) stand condition; 3) herbivore damage; and 4) soil condition can be predicted by lidar-derived structural measures.	1) Partially supported. Ground flora richness demonstrated strong, mostly non-linear, relationships with most of the lidar-derived variables. However, other field-measured biodiversity rarely had any relationship with the lidar variables. 2) Partially supported. Individual measures of stand condition sometimes exhibited strong relationships with lidar-derived variables. However, this was not true for the majority. 3) Not supported. 4) Partially supported. Some soil condition metrics exhibited strong relationships, but only in one of the two transects.	Results presented in this Chapter showed that there were some lidar-derived metrics that could be used to predict some field-collected measures, mainly ground flora species richness. This means that lidar could potentially be used to infer other types of woodland condition values based on the values from Chapter 2. However, other relationships that were present in Chapter 2 were not found in this Chapter. For example, ectomycorrhizal fungi showed a decline over the dieback gradient in Chapter 2, but had little relationships with lidar here.
Chapter 5: The effect of woodland cover on the resilience of a temperate ecosystem (Objective 3)	1) Initial woodland cover influences landscape resilience under different disturbance intensities.	1) Partially supported. For most of the ecosystem properties assessed under the different pulse disturbance intensity scenarios, woodland cover was a significant factor, thus the woodland cover amount influenced the different attributes of resilience, namely resistance, persistence and recovery time. Overall, 73 out of 120 combinations of resilient attributes and scenarios tested had a significant WC term. This number increased to 75 out of 120 when landscapes with no woodland cover were excluded.	The findings in this Chapter showed that overall the amount of initial woodland cover had an effect on resilience. In terms of the New Forest currently, which has approximately 46% woodland cover, resilience is thought to be relatively high for most EPs based on the findings in this Chapter. This is because 50% woodland cover often had the most favourable resilience conditions (i.e. highest resistance and persistence and lowest recovery time) of all hypothetical landscapes simulated.

6.3. Critique of evidence

There were major challenges and other manifest limitations in this research, all of which should be considered when interpreting the results. These are explored below.

6.3.1. Variability

The results from this thesis can only be interpreted for the New Forest, as that was the only study area used. Even though different sites were used within the study area, the variation in pattern, process, climate and condition is likely to be minimal. Therefore, while the knowledge obtained is useful for advising the management of the New Forest, a better understanding of general temperate woodlands resilience could be attained if the experiments and analyses were repeated in other woodlands, as this would increase sampling representatively (Sutherland, 2000).

6.3.2. Application of the resilience concept

Through adoption of the resilience concept of ecosystems and related thinking, the adaptive governance and management framework was created (Sutherland, 2000; Allen et al. 2010). This highlights its crucial use for conservation management in the future as a way of maintaining essential biodiversity, ecosystem functions and ES in ecological and socio-ecological systems (Holling, 1973; Biggs et al. 2012; Standish et al. 2014; Oliver et al. 2015). However, there are still several issues that remain around the application of resilience (Standish et al. 2014; Newton, 2016), with the two most notable being: 1) the main assumption that has to be made and 2) that focusing purely on resilience may simplify complex dynamic ecosystems too much.

The main assumption of both resilience definitions is that stable ecosystem states exist (Holling, 1996b; Liao, 2012). For ecological resilience, this is extended to an assumption that multiple stable states (MSS) exist with a threshold separating two or more equilibrium domains (Holling, 1973; Donohue et al. 2016). However, the MSS theory may not be accurate, as it is difficult to provide evidence for MSS outside laboratory experiments (Schröder et al. 2005; Petraitis, 2013). Furthermore, the MSS assumption misses two important points, namely that thresholds can occur in certain properties or parameters and not lead to transitions to a different state and that change may happen continuously, rather than suddenly (Scheffer et al. 2001; Petraitis et al. 2010; Petraitis, 2013). For engineering resilience, an assumption is made that the system will return to a stable state after a disturbance. As both definitions of resilience in an ecological context therefore rely on this assumption, applying the concepts to real ecological systems may

be highly inaccurate and misleading (Donohue et al. 2016). By assessing individual EPs, rather than ecosystem state, the research in this thesis did not have to rely on the assumptions that the ecosystem was in a stable state. Instead it elucidated how the individual properties changed as a result of disturbance and thus the main assumption did not need to be considered.

Simplification of complex processes by using the resilience concept arises in several ways. First, both ecological and engineering resilience can only be measured in response to an assumed pulse disturbance (Petraitis et al. 2010; Petraitis, 2013; Donohue et al. 2016). Therefore, in Chapter 2, the chronosequence used had to be theoretically measured as time since a disturbance, possibly drought (Mountford and Peterken, 2003; Martin et al. 2015). Similarly, in Chapter 5, engineering resilience had to be measured with respect to a pre-disturbance value (Nimmo et al. 2015). In the latter example, press disturbances (i.e. herbivory) could only be included as a hindrance (or help) to recovery time and persistence subsequent to a pulse disturbance. Consequently, quantification of responses to independent press disturbances using either definition of resilience is not appropriate (Connell and Sousa, 1983; Petraitis, 2013). However, owing to large number of big herbivores exerting high browsing pressure on the New Forest (Newton et al. 2013), it is likely that press disturbances will affect resilience in the future. This needs to be borne in mind when interpreting the results.

Second, scale is important in ecological assessments, both temporally and spatially (Levin, 1992). This is especially true for threshold detection, even though thresholds are often only studied at a single spatial scale (Muradian, 2001; Lindenmayer and Luck, 2005; Groffman et al. 2006; Standish et al. 2014); therefore, careful spatial extrapolation is important (Turner, 1990; Scheffer and Carpenter, 2003). Without considering such complex interaction at different scales there is a risk of not obtaining a full understanding of the multifaceted mechanisms that underpin dynamic ecosystem processes that determine resilience (Liao, 2012; Donohue et al. 2016). In this thesis, empirical values of EPs taken from the stand scale were input into a dynamic model, which simulates succession and other dynamics ecosystem processes. In this way, the mechanisms that influence landscape resilience were incorporated into the experimental design and therefore were accounted for. However, like any model, it was a simplification of natural processes. See section 6.3.6. for more details.

6.3.3. Space-for-time substitution

The experimental design used for Chapter 2 was a space-for-time (SFT) substitution, whereby all of the plots from a single site used in SFTs formed a chronosequence. This technique was used as a necessity, as detailed temporal data for the whole of the New Forest was not available to be able to use such methods as before-after-control-impact methods (e.g. França et al. 2016). In the SFT, spatial data were used for inferring temporal dynamics of a dieback gradient. Even though SFTs are used frequently in terrestrial ecology, especially for land-use change studies (see Johnson and Miyanishi (2008) for examples), several weaknesses can be present based on the assumptions, especially if not tested and validated. Here, each assumption and weakness will be addressed, together with any evidence that supports the assumptions.

The main assumptions of SFT substitutions are that variations in time and space are equivalent (Pickett, 1989) and that the only difference is time since an event, meaning all other conditions are, and have stayed, the same (Johnson and Miyanishi, 2008). Thus, the foremost limitation is the critical assumption that all other conditions are the same across the SFT (Pickett, 1989), i.e. the dieback gradient, in this research. Fukami and Wardle (2005) describe several ways to overcome this limitation. One of these methods was to carry out multi-region comparisons, which are useful for uncovering general trends in ecosystem dynamics. In this study, 12 replicate sites were used to address this. To test that the conditions were the same across all the replicate sites, different conditions were measured pertaining to growing conditions and disturbance, two factors that influence woodland growth and mortality.

It is acknowledged that water availability and any subsequent droughts or waterlogging events are known to damage beech (Peters, 1997; Geßler et al. 2007; Packham et al. 2012; Natural England, 2014), especially in southern England (Peterken and Mountford, 1996; Cavin et al. 2013). The clay content of soil affects how quickly water drains away after a precipitation event. The clay value of the soil could therefore be critical in determining how waterlogged beech stands become. However, across the range of sites used, the percent clay soil content did not change significantly ($F(4,55) = 0.177$, $p = 0.949$) (Fig. 6.1a), based on a one-way ANOVA. Similarly, other variables that could have identified the stands as having different conditions, or being of different ages all showed no significant variation over the gradient. These were: the organic soil depth ($F(4,55) = 1.160$, $p = 0.338$) (Fig. 6.1b), which indicates that similar moisture, nutrients and stability could have been present; soil pH ($F(4,55) = 0.910$, $p = 0.465$) (Fig. 6.1c), which means all the stands were similarly acidic and therefore have the same influence

on process such as nutrient uptake and lichen diversity; and diameter at breast height (DBH) of the remaining living trees (x^2 (3) = 0.586, p = 0.899) (Fig. 6.1d), which indicates that trees were of a similar age and grew in the same competitive conditions. The DBH result was based on the result of a Kruskal-Wallis test as the data were not normally distributed. Overall, the assumption that general conditions are the same is quite well met in the condition metrics examined here. However, possible changes not accounted for could include local climate over the landscape. Climate variation could have affected other sites conditions and disturbance regimes.

Pulse disturbances causing beech mortality in the New Forest have largely been attributed to several droughts and storms that have occurred since the 1970s, with the major drought in 1976 considered to have the most long-lasting impact (Manners and Edwards, 1986; Mountford and Peterken, 2003; Martin et al. 2015). Based on the similar conditions and the proximity of all the sites used, the difference between the size of the disturbance impacts at each site should have hopefully been minute. However, this could still be a source of variation relating to disturbance which was not accounted for. Furthermore, no significant differences across the gradient were exhibited in the herbivore metrics of amount of dung (x^2 (4) = 1.866, p = 0.760) (Fig. 6.2a) and the percentage of holly stand bases that were browsed (F (4,55) = 1.386, p = 0.251) (Fig. 6.2b). The browseline of beech was also ‘very high’ (≥ 80%) over all the sites where it was possible for deer to reach the leaves (< 3 m), with the exception of one plot which had 75% of available leaves eaten, which was classed as high. While these results show that currently the herbivory level is fairly consistent over the gradient, it is difficult to make inferences about how much this has varied since the start of dieback for each site.

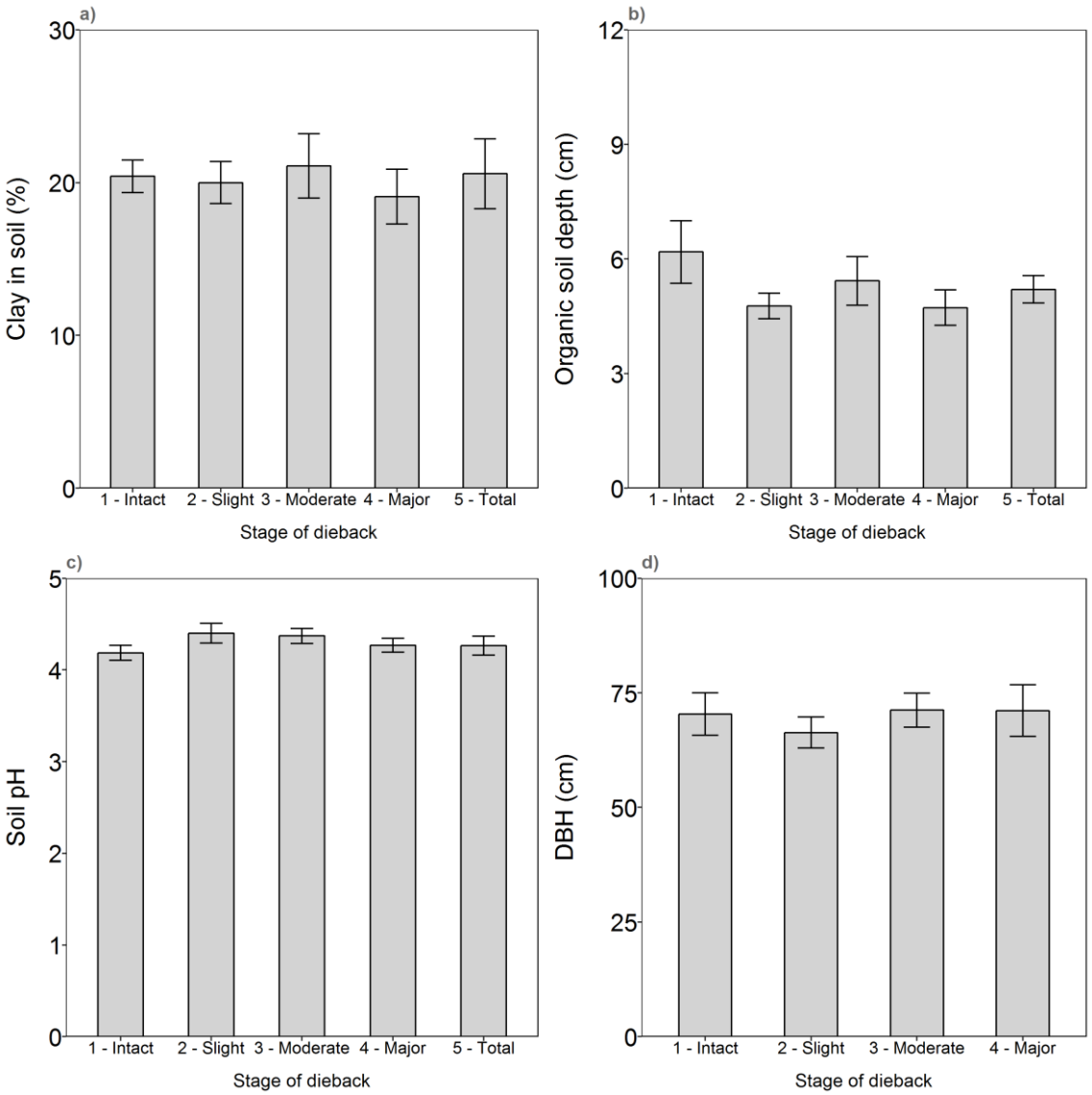

Fig. 6.1: Mean values of a) clay soil content; b) depth of the organic soil layer; c) pH of the soil; and d) diameter at breast height (DBH) of the living beech trees across the gradient of dieback. The black bars indicate the standard error of the mean.

Another solution to overcome any SFT limitations is through the use of long-term observations (Fukami and Wardle, 2005). Therefore, a long-term data set was used that had been recorded over the last 50 years in Denny Wood, which was one of the study areas used in this study. From this complementary data set, it could be established a) that there was a long-term decline in BA in the New Forest, and b) how long that decline took. This allowed inferences to be made of the results from the SFT. Of the stands that declined in BA in Denny Wood, BA decreased linearly on average by just over half (53%) in 50 years, going from 49 m^2 ha^{-1} to 23 m^2 ha^{-1}. On that trajectory, it can be assumed that the time taken between each of the stages of dieback was approximately 25 years (Martin et al. *in press*). However, there was high variation is rate of decline of individual plots.

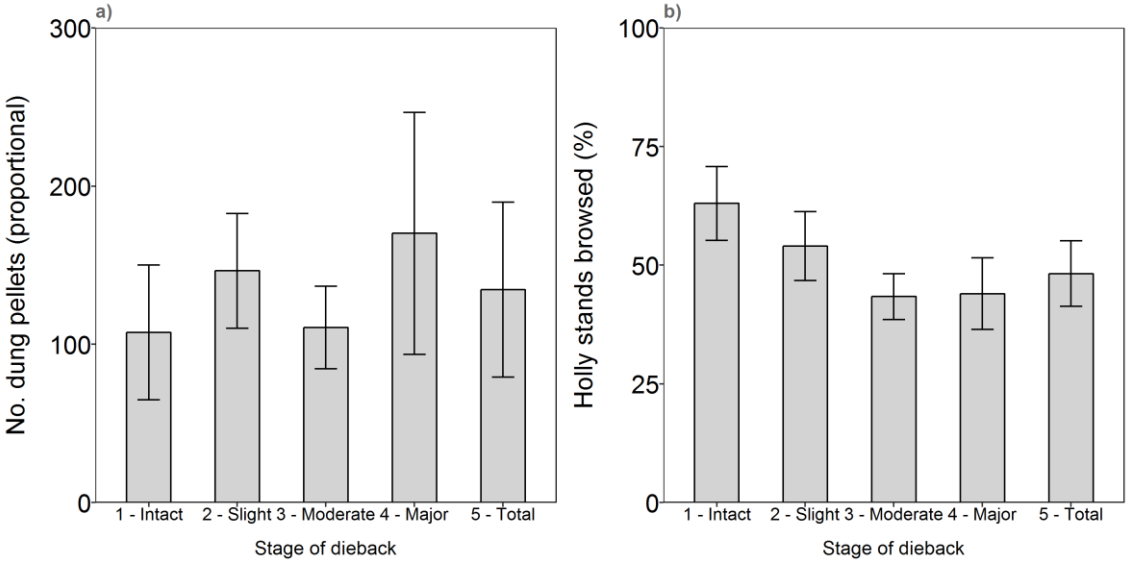

Fig. 6.2: Mean values of a) the total dung count, calculated proportionally (see Appendix 2.1 for method); and b) holly stands browsed across the gradient of dieback. The black bars indicate the standard error of the mean.

Other ways to overcome limitations suggested by Fukami and Wardle (2005) involve field experiments, structural equation modelling and microbial microcosm experiments. However, none of these approaches would have been applicable to the research that was undertaken in this study as they largely relate to testing abiotic gradients (e.g. climate change in Dunne et al. (2004)), and are not feasible for very-long term studies (Fukami and Wardle, 2005). While structural equation modelling has some application, it is mostly used to determine the interactions that influence different properties of an ecosystem, such as carbon storage (Jonsson and Wardle, 2009).

Other potential weaknesses when using SFTs revolve around the inability of the researcher to know if successional processes similarly occurred over time for each site, as reversal (recovery, in this case), alternate pathways and site-specific differences are possibilities that could have occurred (Pickett, 1989). Furthermore, mechanistic models of how all sites would get to the end state and the general dynamics of a system have to been thoroughly known (Pickett, 1989). Fortunately, the important mechanism for temperate forest ecosystems to get from an intact stand to a more grassland state is relatively simple, and largely concerns the death of canopy trees (beech, in this case) (Vera, 2000).

Even though it is not inconceivable that any of the plots studied may recover from its current level of degradation, at the time of surveying it was determined that plots were in the process of declining in BA. This was why one of the criteria for selecting any stages

other than the intact one required either a beech snag or lying dead wood to be present in the plot, and why specifically the 'Total dieback' plots had to contain a beech snag. Nonetheless, there are limitations associated with the last point, as it was difficult to determine when the last standing tree had died. A proxy that could be used is the decay class of the final snag (see Appendix 2.2 for definitions), to give an estimation of time since death. Müller-Using and Bartsch (2009) calculated the average time taken for course woody debris (dead wood) to move to the next decay phase in a beech woodland in Germany. The authors concluded that it took dead wood 3.6 years after death to get to decay phase 2 (6/12 of all 'Total dieback' stages in Chapter 2), 9 years to phase 3 (3/12), 18.1 to decay phase 4 (1/12), and 33.8 years to almost total decay (2/12). The disparity in time since death in all the Total dieback plots may have allowed the underlying processes controlling to have undergone similar disparity in each plot, thus making the same Total dieback stage less directly comparable (Fig. 6.3), which may have affected some of the findings. However, there are a few caveats to also consider: a chronosequence was used in the study of Müller-Using and Bartsch (2009); and the decay phase categories used in that study were slightly different from the ones used in Chapter 2. For example, Müller-Using and Bartsch (2009) did not have a stage 5, so this was inferred above as the longest decay time taken from their work. Furthermore, Přívětivý et al. (2016) showed beech dead wood decay rates differ depending on the climate conditions and the size of the dead wood.

Despite its shortcomings, the use of SFTs in this thesis was extremely useful and considered the optimum way to study a gradient of dieback given the lack of long-term data.

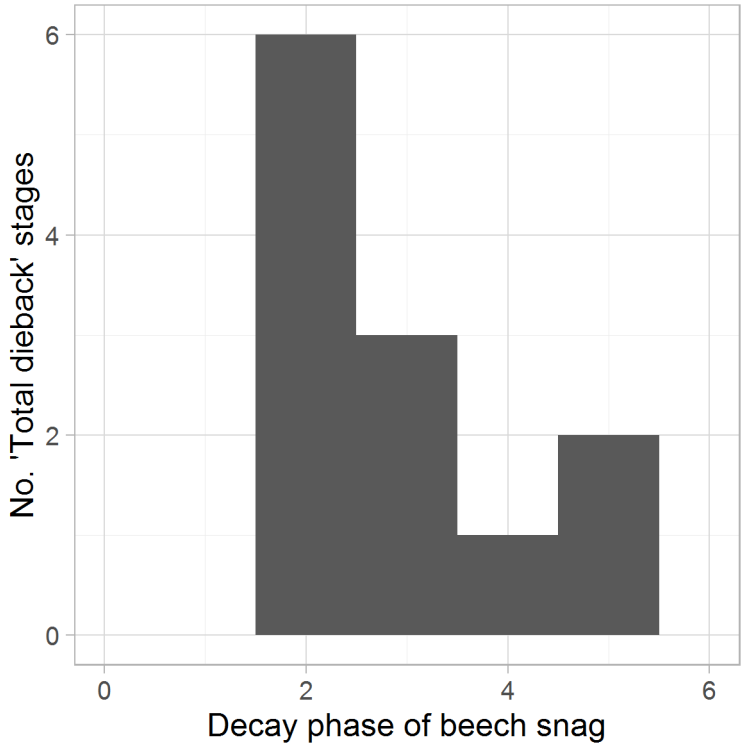

Fig. 6.3: Histogram of which decay phase the last snag was in for all ‘Total dieback’ stages.

6.3.4. Interpretation for CSM targets

The initial part of the experimental design used for Chapter 3 was to assess the condition of the different stages of dieback using published CSM woodland targets specific to the New Forest, as well as one target list that featured more general woodland CSM targets, to determine if CSMs were sensitive to change in condition. This approach had a few limitations and could draw criticism.

First, in the Chapter 3 methodology, each CSM target was assessed with equal weighting. For example, dead wood amount being ‘average’ or ‘good’ was as important as there being at least one native sapling which was as important as there being no signs of safety work. Consequently, for meeting any of these targets, a ‘1’ would be assigned. However, relating to ecology explicitly, it may be considered that the a specific target (e.g. the deadwood volume target) is more important to be met, especially for different taxa (Humphrey et al. 2002; Jabin et al. 2004; Rondeux and Sanchez, 2010; Gao et al. 2014); therefore, in actual assessments more weight may be given to that specific target based on its importance (Fennessey et al. 2007; Falcone et al. 2010), which could have affected the results. Weighting certain targets is recommended in certain frameworks (e.g. Vickerman and Kagan, 2014), and enables better discrimination between the quality of patches (Falcone et al. 2010). Unfortunately, based on the information that was available,

it was unclear whether assessors give weighting to different targets specifically for the New Forest.

Second, CSM targets were recorded differently to how they would be in standard practice – the methodology described in JNCC (2004) suggests a walk-based technique is used, whereas the assessment in Chapter 3 used 20 x 20 m stationary plots. While differences between walk-based visual assessments and plot recordings have been documented (Cantarello and Newton, 2008), the plot-based method used was still representative of conditions of the woodland and therefore appropriate. Moreover, the plot-based technique that used quantitative assessments strengthened assessments, thereby improving consistency and lessening subjectivity of CAs (Gaston et al. 2006; Jackson and Gaston, 2008). Undertaken using JNCC (2004) methodology, the hypotheses tested would have been statistically hard to analyse, and there would have been no meaningful relationships to test the indicators against. Thus, Chapter 3 methodology was specifically designed to be statistically viable, measuring targets and indicators against a confirmed gradient of condition.

6.3.5. Remote sensing approach

There are known limitations to using remote sensing approaches in ecological studies, the most well-known of which is related to the difference between scale of ecological processes and remote-sensing derived resolution (Kerr and Ostrovsky, 2003; Rindfuss et al. 2004; Rocchini et al. 2010; Wang et al. 2010). Nonetheless, when fine-scale lidar data is available and accurate, the results can provide very meaningful and accurate information for ecological studies (Hinsley et al. 2009; Listopad et al. 2015; Réjou-Méchain et al. 2015). Here, even though relationships were found in Chapter 4 at the scale used (i.e. 20 x 20 m; 400 m^2), this does not mean that results would have been similarly inferred if a different scale was used. As pointed out by Levin (1992), heterogeneity and patchiness change over a broad range of scales, which influences the underlying processes and is essential to community organisation and nutrient cycling. Nonetheless, remote sensing is desperately needed for the purpose of analysing changes at appropriate scales (Kerr and Ostrovsky, 2003). In terms of beech woodland dynamics, in a study from Slovenia, small gaps were the most dynamic, with 100 – 300 m^2 being the most frequent and gap sizes $\leq$ 200 m^2 being the driving force in change (Rugani et al. 2013). Similarly, Hobi et al. (2015) showed that gap sizes $\leq$ 200 m^2 were most frequent in primeval Ukraine beech woods. Therefore, for the purposes of using remote sensing (lidar, in Chapter 4) in

beech woods, 400 m^2 should be adequate, at least when identifying surrogate ecological indicators.

Another potential issue specifically for Chapter 4 is that a four-year difference between field and lidar data acquisition could have reduced usability of the data owing to the forest structure changing over that time. To address this point, a Spearman Rank correlation between lidar-derived and field collected canopy openness (considered canopy closure in the lidar data, meaning that there should be a relationship as they are opposing measures) was carried out. This demonstrated that there was a highly significant relationship (r = -0.746, p < 0.001; Fig. 6.4), signifying a good level of usability. However, it is acknowledged that measures of canopy openness are never perfect. For example, a densiometer was used in the field, which was taken at four points in each plot and averaged. This measure can differ depending on weather and subjectivity of the observer (Newton, 2007). Furthermore, the time difference between the different measurements could have meant the more dynamic taxa, such as ECM, were different in 2014 than they were in 2010. There is no way to know how different these measures might have been if both types of data collection were carried out simultaneously, which is often causes issue with remote sensing applications in ecology (Pettorelli et al. 2014).

6.3.6. LANDIS-II model

LANDIS-II model validation

The modelling approach used in Chapter 5 avoided the need for overly complex simulations based on uncertain data such as future climate change; however, a number of important methodological challenges remained. First, validation of simulations is generally required to determine if the model gave a satisfactory level of accuracy (Rosa et al. 2012; Refsgaard et al. 2014). For the LANDIS-II simulations used in Chapter 5 there were no validations for the final outcome. This was partly because: i) the model predicted the future, which is difficult to explore even through large-scale manipulation experiments (Witman and Roy, 2009); and ii) the scenarios started from a hypothetical composition of the New Forest, which excluded conifers. This meant that no realistic data existed or could have been collected for any of the scenarios used. However, in previous research that used the same model parameters and the same study area (the New Forest), validation has been carried out (Newton et al. 2013). Newton et al. (2013) tested the accuracy of LANDIS-II when simulating woodland expansion in the New Forest under high herbivory pressure, the same herbivory pressure that was used for Chapter 5. Through regression analysis, the authors found that there was a significant relationship

between the model-simulated occurrence of different species and the actual number found following a field survey ($r^2 = 0.55$, $p = 0.001$). The model correctly predicted the presence or absence of 25 species. However, the model also predicted the presence of nine species in locations where they were not recorded in reality. Overall, the results of the validation in Newton et al. (2013) seemed to provide a good amount of evidence for the accuracy of using the LANDIS-II model to simulate New Forest dynamics. Furthermore, as the aim of Chapter 5 was to compare the outcomes of differing initial WC scenarios in terms of the different resilience attributes, any inaccuracies should have been the same for each scenario, thereby reducing their impact. Thus, the comparisons should still be valid, even if there are equal uncertainties, and models are an extremely useful way to explore theory and hypotheses in a situation where variables can be controlled.

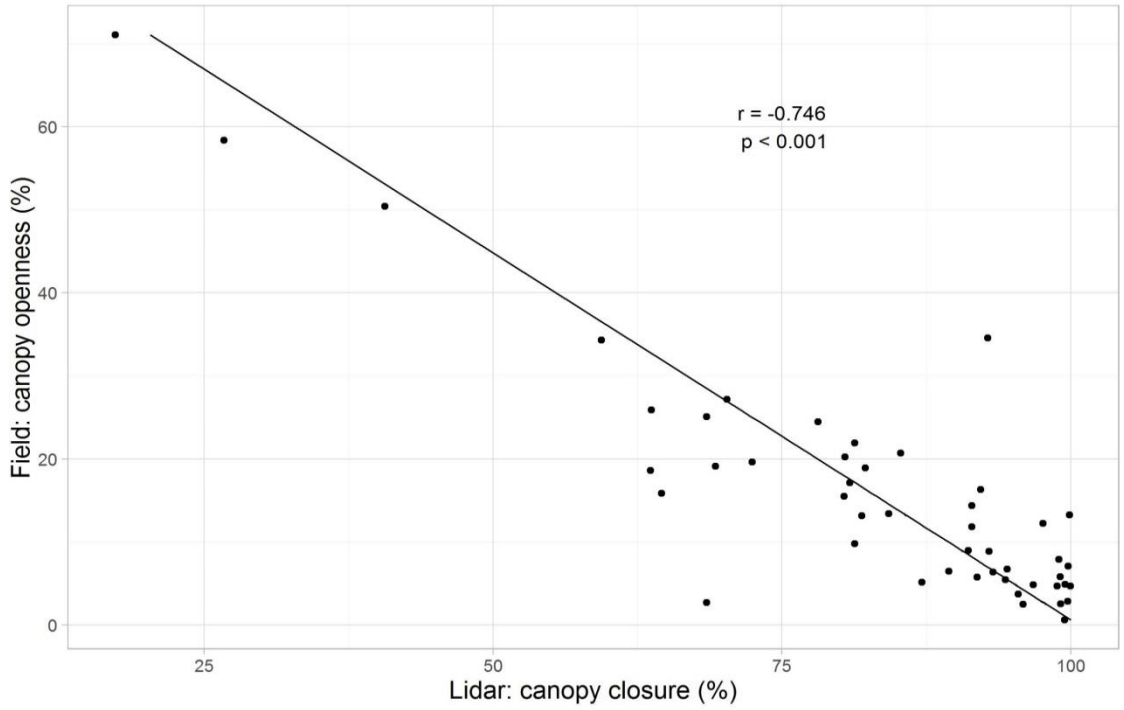

Fig. 6.4: Correlation between lidar-derived measure of canopy closure acquired in 2010 and field-collected canopy openness collected in 2014. The result of a Spearman Rank correlation between the two variables are represented by the *r* and *p* letters, which indicate the correlation coefficient and *p*-value, respectively.

Use of aboveground biomass as a proxy measure

One assumption of Chapter 5 was that a majority of the EPs always showed the same relationship with AGB that they did in Chapter 2, at the stand level. However, the EP values could be influenced by other local aspects rather than simply AGB. Examples of other factors not simulated by the LANDIS-II include: ecological continuity, which is important for plants that disperse poorly (Fedrowitz et al. 2012; Nordén et al. 2014;

Humphrey et al. 2015); legacy effects such of as the loss of mature trees (Seidl et al. 2014a); which can cause a lag in response which may not be recorded for a few years/decades, as seen for population persistence in Lindenmayer and Laurance (2016); dispersal and movement/flow probabilities for AGB-associated EPs (Peay et al. 2010; Craven et al. 2016); and habitat arrangement, which is an often-debated attribute of the persistence of EPs, especially biodiversity. Therefore, future research that incorporates these factors together with the findings in this study would be beneficial in advancing knowledge regarding landscape resilience.

6.3.7. Selection of ecosystem properties and indicators assessed

In this thesis, the resilient attributes of a diverse range of important EPs were measured. Obviously, this did not include all EPs. For example, in terms of biodiversity, only one type of fauna was assessed, namely ground-dwelling invertebrates. However, other indicators could have been used, such as mammals, reptiles and birds and/or rare species (e.g. Red Book species that are found in New Forest (Tubbs, 2001; Newton, 2010)), all of which are commonly used in forest studies (Gao et al. 2015). Nonetheless, flora and fauna that are disadvantaged in some way should be assessed as a priority (Noss, 1999), as they have less chance of recovery from surrounding habitats. Disadvantaged taxa include those that are limited by dispersal distance, resource availability or other factors. Lichens, vascular plants, and fungi, which were recorded in this thesis, are all examples of limited taxa (Sillett et al. 2000; Berglund and Jonsson, 2005; Paltto et al. 2011). Moreover, this research included monitoring aspects of each of the three attributes that provide a framework for assessing woodland biodiversity and condition, namely composition, structure and function (Noss, 1999; Gao et al. 2015; Lawley et al. 2016). Therefore, the metrics used should be sufficient to determine the condition of any woodland.

One additional factor that could be assessed in further work that is relevant both at the scale studied and for the three woodland ecosystem condition attributes is soil biodiversity. Soil fauna may represent as much as 23% of all biodiversity (Lavelle et al. 2006). Moreover, they are critical to the provision of ES and ecosystem functioning, having active roles in nutrient cycling, soil formation, carbon stabilisation and primary productivity (Lavelle et al. 2006; de Vries et al. 2013). Soil engineers, such as earthworms, interact with fungi to influence the structure and functioning of the soil (Jouquet et al. 2006; de Vries et al. 2013; Lavelle et al. 2016). Therefore, studying the

soil and the interactions inside it may provide more knowledge about feedbacks that contribute to resilience of woodlands.

For three of the Chapters (2-4) in this thesis, measurements mostly related to the state of an EP or its change. However, indicator frameworks suggest that factors that affect the state of EPs need to be considered as well (Stork et al. 1997; EEA, 2002; Niemeijer and de Groot, 2008). Such factors are part of DPSIR (drivers, pressures, state, impact and response) indicator frameworks (EEA, 2002). In the frameworks, drivers are the underlying human or natural factors that cause change either directly or indirectly to the environment (EEA, 2002; MEA, 2005; Newton, 2007). Drivers cause the pressures, which in forests can include logging, grazing, pollution or fragmentation (Stork et al. 1997). This affects the state from which the impact (i.e. change) can be determined, if previous data is available. Finally, response describes the decisions made in response to the impacts, which often involves trying to change the drivers or pressures or to try and improve state (Newton, 2007; Niemeijer and de Groot, 2008; Maxim et al. 2009).

While drivers and pressures were not assessed directly in Chapters 2-4 they were alluded to. For example, it is noted that dieback of the New Forest is likely to be driven by historic drought, pathogen spread, excessive herbivory or climate change (Mountford and Peterken, 2003; Newton, 2010; Martin et al. 2015). Thus, part of the reason that drivers were not measured were: i) it is unknown precisely what is causing large-scale mortality in the New Forest; ii) drivers are thought to have happened historically (e.g. drought); and iii) the experimental design was created specifically to determine the state and impact, which results from the pressure of dieback. Moreover, in Chapter 5, drivers and pressures were an integral part of the design, with the simulated pulse and press disturbances used representing pathogen attack and excessive herbivory, respectively. As the simulations were run using LANDIS-II the changing C and N cycles, which could act as pressures in themselves (Stork et al. 1997), were incorporated, also.

One driver that was not accounted for at all in this thesis was climate change. Climate change is likely to affect the future composition and structure of the forest, especially the A&O woodlands (Grant and Edwards, 2008; Martin et al. 2015). The lack of simulation of changing climate has a major impact on conclusions that could be drawn from Chapter 5. Climate change is already affecting growth and regeneration of European forests, with beech being particularly afflicted (Campioli et al. 2012; Kint et al. 2012). In the future, under climate change extreme events such as extended drought periods and strong storms will likely be more frequent (Breda et al. 2006; Lindner et al. 2010; Scheller et al. 2012), pathogen attack will be more regular (Jung et al 2009), and forest ES

provisions will likely be highly modified (Briner et al. 2013). Thus, including climate change in simulations could change the outcome considerably (Schuler et al. 2016), with the modified interactions between disturbances affecting the resilience of forests (Anderson-Teixeira et al. 2013). Even with this knowledge, there is great difficulty in modelling the uncertainties that climate change predictions could bring (Lindner et al. 2010, 2014), which increases the chance of arriving at the wrong conclusions. Therefore, despite not including climate change, the results from Chapter 5 still contribute to their intended aim, which was to determine how different initial WC influenced resilience. However, including climate change in simulations would be extremely useful, as long as the associated uncertainty was also considered (Lindner et al. 2014; Schuler et al. 2016).

6.4. Suggestions for future research

There are several ways to build upon the knowledge regarding resilience of woodlands and associated properties that was obtained from this thesis, which can be broken down into four categories: expanding the experimental design; resilience at the stand scale; resilience at the landscape scale; and resilience assessments and surrogates.

The experimental design category largely relates to repeating measurements over time and in space. First, the analyses that were undertaken could be repeated in other temperate woodlands, as this would reduce the chance of natural variability impacting the findings (Ford, 2000; Sutherland, 2000; Newton, 2007), thereby increasing information about woodland resilience in a broader sense. Experimental design could also extend to repeating measurements of ecological variables over longer time scales. As a majority of EP data were only collected from a single point in time, some variation in ecosystem functions and biodiversity between different seasons and subsequent years may have been missed (Ford, 2000; Newton, 2007). Repeated measurements over time could also be carried out for the individual sites themselves. While the criteria used hopefully meant that sites measured were dying back for Chapter 2, the only way to be sure of this is to continue measurements in time to assess whether they degrade further or show signs of recovering. This could even be potentially undertaken through the use of remote sensing, to a certain degree (Newton, 2007; Pettorelli et al. 2014). Lastly, more could be deduced about resilience from long-term data sets. This would mean that chronosequences would not have to be relied on when testing for the existence of thresholds over time (Fukami and Wardle, 2005). However, there are manifest challenges with setting up long-term plots, which include finding appropriate locations that are not managed, having the

resources available for continual monitoring and, most challenging of all, predicting which stands are likely to be affected by disturbance in the future.

Many authors note that negative feedbacks switching to positive feedbacks are the underlying mechanistic change that creates thresholds (e.g. Briske et al. 2010). Research on feedbacks however is, like most threshold work, still largely theoretical with little empirical evidence in terrestrial systems. Therefore, to further enhance knowledge of resilience at the stand scale, EPs from Chapter 2 that exhibited thresholds could be compared to other ecosystem factors. This would allow elucidation of possible changing feedbacks that caused an EP to exceed a threshold. For example, a gradient of woodland ECM richness (i.e. a threshold EP) could be found, over which soil biology and chemistry, factors hypothesised to contribute to the changing feedbacks for ECM, could be measured across to determine if changes occur prior to the to the value at which ECM exceeded a threshold. Such experiments may also provide evidence for multiple, sequential structural, biodiversity and functioning thresholds, a prospect that currently lacks evidence, but that would have major implications. See Briske et al. (2006), Kinzig et al. (2006) and Mumby et al. (2011) for more details.

At the landscape scale, resilience was measured based on hypothetical models that focused specifically on the cover of broadleaved woodlands. This metric was a measure of structural connectivity. In future research, a range of other landscape factors that pertain more to functional connectivity could be analysed to reveal more about what makes woodland EPs resilient at the landscape level (Oliver et al. 2015). Landscape functional connectivity factors such as the capacity and probability of dispersal or movement success of biodiversity or ES (Goodwin, 2003; Estreguil et al. 2013; Tambosi et al. 2014) could be included in analysis, as could the effect of habitat fragmentation on different species or taxa (Fahrig, 2003; Newton, 2007; Broadbent et al. 2008). However, this would involve collecting a lot of data if it were to cover a similar number of EPs that were assessed in Chapter 5. Additionally, greater cultural ecosystem services could be included in future assessments, as the New Forest is a socio-ecological ecosystem that is, and has historically been, highly influenced by people.

Climate change was not directly measured or included in this thesis. However, beech stands are susceptible to changes in climate, as are most temperate ecosystems and their biodiversity. Nonetheless, many knowledge gaps remain around the impact that climate change will have on the resilience of natural communities and the disturbances that biodiversity may have to be resilient to (Côté and Darling, 2010; Moritz et al. 2012; Moritz and Agudo, 2013; Lindner et al. 2014). Therefore, resilience research in the future

should incorporate climate change scenarios, noting the associated uncertainties, and include factors such as forest species recruitment, which is an essential part of resilience (Lindner et al. 2014).

Regarding resilience assessments, which are supposed to enable accurate inference of the current level of resilience (Carpenter et al. 2001; Bennett et al. 2005; Quinlan et al. 2016), indicators that are appropriate to infer woodland resilience needs a lot of attention to be better able to elucidate useful surrogate ecological measures that i) are sensitive to changing condition and 2) can be assessed with limited time and financial resources. For ground-based assessments, this could include more exploration of the key aspects that will enable the differentiation of condition to become clear, and could also include a weighting system for the different indicators (Oliver et al. 2014). For remote sensing assessments, the next step is to carry out a similar assessment to the tests carried out in the thesis but with no time lag between lidar and field data collection, or possibly even collect both frequently over a temporal time period to be able to infer exactly when the relationships change between the two sets of data.

6.5. Conclusion

The work presented in this thesis has enhanced knowledge of temperate woodland resilience at different scales and given an insight into the effectiveness of condition assessment tools that may be importantly utilised to carry out resilience assessments and conservation activities in the future. It is hoped that the research from this PhD will be incorporated by policymakers, researchers and managers alike to produce plans and work that will enhance both the overall resilience of these special ecosystems and improve the effectiveness of woodland condition assessments in the future.

References

Adam, T. C., Schmitt, R. J., Holbrook, S. J., Brooks, A. J., Edmunds, P. J., Carpenter, R. C. and Bernardi, G., 2011. Herbivory, connectivity, and ecosystem resilience: response of a coral reef to a large-scale perturbation. *PLoS ONE*, 6 (8), e23717.

Adams, M. A., 2013. Mega-fires, tipping points and ecosystem services: managing forests and woodlands in an uncertain future. *Forest Ecology and Management*, 294, 250-261.

Ahmed, A., 2008. *Underlying causes of deforestation and forest degradation in Bangladesh* [online]. Amsterdam, Netherlands: Global Forest Coalition.

Alencar, A. A., Brando, P. M., Asner, G. P. and Putz, F. E., 2015. Landscape fragmentation, severe drought, and the new Amazon forest fire regime. *Ecological Applications*, 25 (6), 1493-1505.

Allan, J. R., Venter, O., Maxwell, S., Bertzky, B., Jones, K., Shi, Y. and Watson, J. E. M., 2017. Recent increases in human pressure and forest loss threaten many natural world heritage sites. *Biological Conservation*, 206, 47-55.

Allen, C. D., Birkeland, C., Chapin III, F. S., Groffman, P. M., Guntenspergen, G. R., Knapp, A. K., McGuire, A. D., Mulholland, P. J., Peters, D.P.C., Roby, D.D. and Sugihara, G., 2009. *Thresholds of climate change in ecosystems: final report, synthesis and assessment product 4.2*. Lincoln, Nebraska, USA: U.S. Geological Survey. Paper 13.

Allen, C. D., Breshears, D. D. and McDowell, N. G., 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, 6 (8), 1-55.

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D. D. and Hogg, E. T., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, 259 (4), 660-684.

Allen, C. R., Angeler, D. G., Cumming, G. S., Folke, C., Twidwell, D. and Uden, D. R., 2016. Quantifying spatial resilience. *Journal of Applied Ecology*, 53 (3), 625-635.

Allen, C. R., Fontaine, J. J., Pope, K. L. and Garmestani, A. S., 2011. Adaptive management for a turbulent future. *Journal of Environmental Management*, 92 (5), 1339-1345.

Altieri, M. A., Nicholls, C. I., Henao, A. and Lana, M. A., 2015. Agroecology and the design of climate change-resilient farming systems. *Agronomy for Sustainable Development*, 35 (3), 869-890.

Anderegg, W. R. L., Plavcová, L., Anderegg, L. D. L., Hacke, U. G., Berry, J. A. and Field, C. B., 2013. Drought's legacy: multiyear hydraulic deterioration underlies widespread aspen forest die-off and portends increased future risk. *Global Change Biology*, 19 (4), 1188-1196.

Anderies, J. M., Carpenter, S., Steffen, W. and Rockström, J., 2013. The topology of non-linear global carbon dynamics: from tipping points to planetary boundaries. *Environmental Research Letters*, 8 (4), 44-48.

Anderson-Teixeira, K. J., Miller, A. D., Mohan, J. E., Hudiburg, T. W., Duval, B. D. and DeLucia, E. H., 2013. Altered dynamics of forest recovery under a changing climate. *Global Change Biology*, 19 (7), 2001-2021.

Angelstam, P. K., 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. *Journal of Vegetation Science*, 9 (1), 593-602.

Angelstam, P. and Dönz-Breuss, M., 2004. Measuring forest biodiversity at the stand scale: An evaluation of indicators in European forest history gradients. *Ecological Bulletins*, 51, 305-332.
Aplin, P., 2005. Remote sensing: ecology. *Progress in Physical Geography*, 29 (1), 104-113.
Armesto, J. J. and Martinez, J. A., 1978. Relations between vegetation structure and slope aspect in the Mediterranean region of Chile. *Journal of Ecology*, 66, 881-889.
Ashman, M. and Puri, G., 2008. *Essential soil science: a clear and concise introduction to soil science.* Oxford, UK: Wiley-Blackwell.
Asner, G. P., Mascaro, J., Muller-Landau, H. C., Vieilledent, G., Vaudry, R., Rasamoelina, M., Hall, J. S. and van Breugel, M., 2012. A universal airborne lidar approach for tropical forest carbon mapping. *Oecologia*, 168 (4), 1147-1160.
Attiwill, P. M. and Adams, M. A., 1993. Nutrient cycling in forests. *New Phytologist*, 124 (4), 561-582.
Avila, J. M., Gallardo, A., Ibáñez, B. and Gómez-Aparicio, L., 2016. *Quercus suber* dieback alters soil respiration and nutrient availability in Mediterranean forests. *Journal of Ecology*, 104 (5), 1441–1452.
Ayram, C. A. C., Mendoza, M. E., Etter, A. and Salicrup, D. R. P., 2016. Habitat connectivity in biodiversity conservation: a review of recent studies and applications. *Progress in Physical Geography*, 401 (1), 7-37.
Bailey, S., 2007. Increasing connectivity in fragmented landscapes: an investigation of evidence for biodiversity gain in woodlands. *Forest Ecology and Management*, 238 (1), 7-23.
Balmford, A., Rodrigues, A., Walpole, M., Ten Brink, P., Kettunen, M., Braat, L. and de Groot, R., 2008. *Review on the economics of biodiversity loss: scoping the science*. Cambridge, UK: European Commission. ENV/070307/2007/486089/ETU/B2.
Balvanera, P., Pfisterer, A. B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D. and Schmid, B., 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, 9 (10), 1146-1156.
Barbosa, J.M. and Asner, G.P., 2017. Prioritizing landscapes for restoration based on spatial patterns of ecosystem controls and plant–plant interactions. *Journal of Applied Ecology*.
Barnosky, A. D., Hadly, E. A., Bascompte, J., Berlow, E. L., Brown, J. H., Fortelius, M., Getz, W. M., Harte, J., Hastings, A., Marquet, P. A., Martinez, N. D., Mooers, A., Roopnarine, P., Vermeij, G., Williams, J. W., Gillespie, R., Kitzes, J., Marshall, C., Matzke, N., Mindell, D. P., Revilla, E. and Smith, A. B., 2012. Approaching a state shift in Earth's biosphere. *Nature*, 486 (7401), 52-58.
Bartels, S. F., Chen, H. Y., Wulder, M. A. and White, J. C., 2016. Trends in post-disturbance recovery rates of Canada's forests following wildfire and harvest. *Forest Ecology and Management*, 361, 194-207.
Bartoń, K., 2014. *MuMIn: Multi-model inference* [online]. R package version 1.10.0. Available from: https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf [Accessed March 2015].
Bater, C. W., Coops, N. C., Gergel, S. E., LeMay, V. and Collins, D., 2009. Estimation of standing dead tree class distributions in northwest coastal forests using lidar remote sensing. *Canadian Journal of Forest Research*, 39 (6), 1080-1091.
Bates, D., Maechler, M., Bolker, B. and Walker, S., 2013. *Lme4: linear mixed-effects models using Eigen and S4* [online]. R package version 1.0-5.

Begon, M., Telfer, S., Smith, M. J., Burthe, S., Paterson, S. and Lambin, X., 2009. Seasonal host dynamics drive the timing of recurrent epidemics in a wildlife population. *Proceedings of the Royal Society B: Biological Sciences,* 276 (1662), 1603-1610.

Beisner, B. E., 2012. The shifting states of resilience: easier to define than to measure. *Ideas in Ecology and Evolution,* 5, 57–62.

Beisner, B. E., Haydon, D. T. and Cuddington, K., 2003. Alternative stable states in ecology. *Frontiers in Ecology and the Environment,* 1 (7), 376-382.

Beller, E., Robinson, A., Grossinger, R. and Grenier, L., 2015. *Landscape resilience framework: operationalizing ecological resilience at the landscape scale* [Online]. Richmond, California, USA: San Francisco Estuary Institute. A Report of SFEI-ASC's Resilient Landscapes Program No752. Available from: http://resilientsv.sfei.org/sites/default/files/general_content/SFEI_2015_Landscape%20Resilience%20Framework.pdf [Accessed: May 2016].

Bennett, E. M., Cumming, G. S. and Peterson, G. D., 2005. A systems model approach to determining resilience surrogates for case studies. *Ecosystems,* 8 (8), 945-957.

Berglund, H. and Jonsson, B. G., 2005. Verifying an extinction debt among lichens and fungi in northern Swedish boreal forests. *Conservation Biology,* 19 (2), 338-348.

Bergmeier, E., Petermann, J. and Schröder, E., 2010. Geobotanical survey of wood-pasture habitats in Europe: diversity, threats and conservation. *Biodiversity and Conservation,* 19 (11), 2995-3014.

Bergström, R. and Guillet, C., 2002. Summer browsing by large herbivores in short-rotation willow plantations. *Biomass and Bioenergy,* 23 (1), 27-32.

Berry, P. M., Dawson, T. P., Harrison, P. A. and Pearson, R. G., 2002. Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. *Global Ecology and Biogeography,* 11 (6), 453-462.

Biggs, R., Schlüter, M., Biggs, D., Bohensky, E. L., Burnsilver, S., Cundill, G., Dakos, V., Daw, T. M., Evans, L. S., Kotschy, K., Leitch, A. M., Meek, C., Quinlan, A., Raudsepp-Hearne, C., Robards, M. D., Schoon, M. L., Schultz, L. and West, P. C., 2012. Toward principles for enhancing the resilience of ecosystem services. *Annual Review of Environment and Resources,* 37 (1), 421-448.

Binkley, D. and Fisher, R., 2012. *Ecology and management of forest soils.* New York, USA: John Wiley and Sons.

Bodin, Ö. and Prell, C., 2011. *Social networks and natural resource management: uncovering the social fabric of environmental governance.* Cambridge, UK: Cambridge University Press.

Bodin, Ö., Tengö, M., Norman, A., Lundberg, J. and Elmqvist, T., 2006. The value of small size: loss of forest patches and ecological thresholds in southern Madagascar. *Ecological Applications,* 16 (2), 440-451.

Bonan, G. B., 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science,* 320 (5882), 1444-1449.

Booth, M. S., Stark, J. M. and Rastetter, E., 2005. Controls on nitrogen cycling in terrestrial ecosystems: a synthetic analysis of literature data. *Ecological Monographs,* 75 (2), 139-157.

Bottero, A., Garbarino, M., Dukic, V., Govedar, Z., Lingua, E., Nagel, T. and Motta, R., 2011. Gap-phase dynamics in the old-growth forest of Lom, Bosnia and Herzegovina. *Silva Fennica,* 45 (5), 875-887.

Bouget, C., Larrieu, L. and Brin, A., 2014. Key features for saproxylic beetle diversity derived from rapid habitat assessment in temperate forests. *Ecological Indicators,* 36, 656-664.

Brand, F. S. and Jax, K., 2007. Focusing the meaning (s) of resilience: resilience as a descriptive concept and a boundary object. *Ecology and Society,* 12 (1), 23.

Bréda, N., Huc, R., Granier, A. and Dreyer, E., 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science,* 63 (6), 625-644.

Breshears, D. D., Cobb, N. S., Rich, P. M., Price, K. P., Allen, C. D., Balice, R. G., Romme, W. H., Kastens, J. H., Floyd, M. L., Belnap, J., Anderson, J. J., Myers, O. B. and Meyer, C. W., 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America,* 102 (42), 15144-15148.

Breshears, D. D., Myers, O. B., Meyer, C. W., Barnes, F. J., Zou, C. B., Allen, C. D., McDowell, N. G. and Pockman, W. T., 2009. Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. *Frontiers in Ecology and the Environment,* 7 (4), 185-189.

Briner, S., Elkin, C. and Huber, R., 2013. Evaluating the relative impact of climate and economic changes on forest and agricultural ecosystem services in mountain regions. *Journal of Environmental Management,* 129 (1), 414-422.

Briske, D. D., Fuhlendorf, S. D. and Smeins, F., 2006. A unified framework for assessment and application of ecological thresholds. *Rangeland Ecology and Management,* 59 (3), 225-236.

Briske, D. D., Washington-Allen, R. A., Johnson, C. R., Lockwood, J. A., Lockwood, D. R., Stringham, T. K. and Shugart, H. H., 2010. Catastrophic thresholds: a synthesis of concepts, perspectives, and applications. *Ecology and Society,* 15 (3), 1-12.

Broadbent, E. N., Asner, G. P., Keller, M., Knapp, D. E., Oliveira, P. J. and Silva, J. N., 2008. Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. *Biological Conservation,* 141 (7), 1745-1757.

Brockerhoff, E. G., Jactel, H., Parrotta, J. A. and Ferraz, S. F. B., 2013. Role of eucalypt and other planted forests in biodiversity conservation and the provision of biodiversity-related ecosystem services. *Forest Ecology and Management,* 301, 43-50.

Brook, B. W., Ellis, E. C., Perring, M. P., Mackay, A. W. and Blomqvist, L., 2013. Does the terrestrial biosphere have planetary tipping points? *Trends in Ecology and Evolution,* 28 (7), 396-401.

Brook, B. W., Sodhi, N. S. and Ng, P. K. L., 2003. Catastrophic extinctions follow deforestation in Singapore. *Nature,* 424 (6947), 420-426.

Brown, J. M. B., 1953. *Studies on British beechwoods.* West Bromwich, UK: Forestry Commission. Forestry Commission Bulletin No. 20.

Burnham, K. P. and Anderson, D. R., 2002. *Model Selection and multimodel inference.* New York, USA: Springer-Verlag.

Burrell, G.A. and Seibert, F.M., 1916. *Gases found in coal mines. Miner's circular no. 14.* Washington, D. C., USA: US Department of the Interior, Bureau of Mines.

Butchart, S. H. M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J. P. W., Almond, R. E. A., Baillie, J. E. M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K. E., Carr, G. M., Chanson, J., Chenery, A. M., Csirke, J., Davidson, N. C., Dentener, F., Foster, M., Galli, A., Galloway, J. N., Genovesi, P., Gregory, R. D., Hockings, M., Kapos, V., Lamarque, J.-F., Leverington, F., Loh, J., McGeoch, M. A., McRae, L., Minasyan, A., Morcillo, M. H., Oldfield, T. E. E., Pauly, D., Quader, S., Revenga, C., Sauer, J. R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S. N., Symes, A., Tierney, M., Tyrrell, T. D., Vié, J.-C. and Watson, R., 2010. Global biodiversity: indicators of recent declines. *Science,* 328 (5982), 1164-1168.

Buttolph, L. P. and Coppock, D. L., 2004. Influence of deferred grazing on vegetation dynamics and livestock productivity in an Andean pastoral system. *Journal of Applied Ecology,* 41 (4), 664-674.

Cameron, A. C. and Trivedi, P. K., 2013. *Regression analysis of count data.* Cambridge, UK: Cambridge University Press.

Camisón, Á., Miguel, R., Marcos, J. L., Revilla, J., Tardáguila, M. Á., Hernández, D., Lakicevic, M., Jovellar, L. C. and Silla, F., 2015. Regeneration dynamics of *Quercus pyrenaica* willd. In the central system (Spain). *Forest Ecology and Management,* 343, 42-52.

Campioli, M., Vincke, C., Jonard, M., Kint, V., Demarée, G. and Ponette, Q., 2012. Current status and predicted impact of climate change on forest production and biogeochemistry in the temperate oceanic European zone: review and prospects for Belgium as a case study. *Journal of Forest Research*, 17 (1), 1-18.

Cantarello, E. and Newton, A. C., 2008. Identifying cost-effective indicators to assess the conservation status of forested habitats in Natura 2000 sites. *Forest Ecology and Management,* 256 (4), 815-826.

Cantarello, E., Newton, A. C., Martin, P. A., Evans, P. M., Gosal, A. and Lucash, M. S., 2017. Quantifying future resilience of a temperate forest undergoing dieback. *In press*.

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S. and Naeem, S., 2012. Biodiversity loss and its impact on humanity. *Nature,* 486 (7401), 59-67.

Carlsson, A. L., Bergfur, J. and Milberg, P., 2005. Comparison of data from two vegetation monitoring methods in semi-natural grasslands. *Environmental Monitoring and Assessment,* 100 (1-3), 235-248.

Carpenter, S., Folke, C., Scheffer, M. and Westley, F., 2009. Resilience: accounting for the noncomputable. *Ecology and Society*, 14 (1), article 13.

Carpenter, S., Walker, B., Anderies, J. M. and Abel, N., 2001. From metaphor to measurement: resilience of what to what? *Ecosystems,* 4 (8), 765-781.

Carpenter, S., Westley, F. and Turner, M. G., 2005. Surrogates for resilience of social–ecological systems. *Ecosystems*, 8 (8), 941-944.

Carvalho, J., Silva, J. N. and Lopes, J.D., 2004. Growth rate of a terra firme rain forest in Brazilian Amazonia over an eight-year period in response to logging. *Acta Amazonica*, 34 (2), 209-217.

Casini, M., Hjelm, J., Molinero, J.-C., Lövgren, J., Cardinale, M., Bartolino, V., Belgrano, A. and Kornilovs, G., 2009. Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. *Proceedings of the National Academy of Sciences,* 106 (1), 197-202.

Catalan, J., Barbieri, M. G., Bartumeus, F., Bitušík, P., Botev, I., Brancelj, A., Cogălniceanu, D. A. N., Manca, M., Marchetto, A., Ognjanova-Rumenova, N., Pla, S., Rieradevall, M., Sorvari, S., Štefková, E., Stuchlík, E. and Ventura, M., 2009. Ecological thresholds in European alpine lakes. *Freshwater Biology,* 54 (12), 2494-2517.

Cavin, L. and Jump, A. S., 2016. Highest drought sensitivity and lowest resistance to growth suppression are found in the range core of the tree *Fagus sylvatica* L. not the equatorial range edge. *Global Change Biology*, 23 (1), 362-379.

Cavin, L., Mountford, E. P., Peterken, G. F. and Jump, A. S., 2013. Extreme drought alters competitive dominance within and between tree species in a mixed forest stand. *Functional Ecology,* 27 (6), 1424-1435.

Chazdon, R. L., 2008. Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science,* 320 (5882), 1458-1460.

Chen, J., John, R., Sun, G., McNulty, S., Noormets, A., Xiao, J., Turner, M. G. and Franklin, J. F., 2014. Carbon fluxes and storage in forests and landscapes. *In:* Azevedo, J. C., Perera, A. H., and Pinto, M. A., eds. *Forest landscapes and global change: challenges for research and management*. New York, USA: Springer New York, 139-166.

Churski, M., Bubnicki, J. W., Jędrzejewska, B., Kuijper, D. P. J. and Cromsigt, J. P. G. M., 2017. Brown world forests: increased ungulate browsing keeps temperate trees in recruitment bottlenecks in resource hotspots. *New Phytologist,* 214 (1), 158-168.

COAG, 2011. *National strategy for disaster resilience: building our nation's resilience to disasters* [online]. Australian Government. Available from: https://www.ag.gov.au/EmergencyManagement/Documents/NationalStrategyforDisasterResilience.PDF [Accessed March 2016].

Cole, L. E. S., Bhagwat, S. A. and Willis, K. J., 2014. Recovery and resilience of tropical forests after disturbance. *Nature Communications,* 5, 3906.

Connell, J. H. and Slatyer, R. O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist,* 111 (982), 1119-1144.

Connell, J. H. and Sousa, W. P., 1983. On the evidence needed to judge ecological stability or persistence. *The American Naturalist,* 121 (6), 789-824.

Connell, S. D., Nimmo, D. G., Ghedini, G., Mac Nally, R. and Bennett, A. F., 2016. Ecological resistance–why mechanisms matter: a reply to Sundstrom et al. *Trends in Ecology and Evolution,* 31 (6), 413-414.

Cook, R. L., Binkley, D., Mendes, J. C. T. and Stape, J. L., 2014. Soil carbon stocks and forest biomass following conversion of pasture to broadleaf and conifer plantations in southeastern Brazil. *Forest Ecology and Management, 324,* 37-45.

Coops, N. C., Tompaski, P., Nijland, W., Rickbeil, G. J. M., Nielsen, S. E., Bater, C. W. and Stadt, J. J., 2016. A forest structure habitat index based on airborne laser scanning data. *Ecological Indicators,* 67, 346-357.

Coops, N. C., Varhola, A., Bater, C. W., Teti, P., Boon, S., Goodwin, N. and Weiler, M., 2009. Assessing differences in tree and stand structure following beetle infestation using lidar data. *Canadian Journal of Remote Sensing,* 35 (6), 497-508.

Corcobado, T., Moreno, G., Azul, A. M. and Solla, A., 2015. Seasonal variations of ectomycorrhizal communities in declining *Quercus ilex* forests: interactions with topography, tree health status and *Phytophthora cinnamomi* infections. *Forestry,* 88 (2), 257-266.

Cordingley, J. E., Newton, A. C., Rose, R. J., Clarke, R. T. and Bullock, J. M., 2015. Habitat fragmentation intensifies trade-offs between biodiversity and ecosystem services in a heathland ecosystem in southern England. *PLoS ONE,* 10 (6), e0130004.

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R. V., Paruelo, J., Raskin, R. G., Sutton, P. and van den Belt, M., 1998. The value of the world's ecosystem services and natural capital. *Ecological Economics,* 25 (1), 3-15.

Côté, I. M. and Darling, E. S., 2010. Rethinking ecosystem resilience in the face of climate change. *PLoS Biology,* 8 (7), e1000438.

Cox, D. R. and Snell, E. J., 1989. *Analysis of binary data.* California, USA: CRC Press.

Craven, D., Filotas, E., Angers, V. A. and Messier, C., 2016. Evaluating resilience of tree communities in fragmented landscapes: linking functional response diversity with landscape connectivity. *Diversity and Distributions,* 22 (5), 505-518.

Crann, S. E., Fairley, C., Badulescu, D., Mohn, W. W. and O'Doherty, K. C., 2015. Soils, microbes, and forest health: a qualitative analysis of social and institutional factors affecting genomic technology adoption. Technology in Society, 43, 1-9.

Cribari-Neto, F. and Zeileis, A., 2010. Beta regression in r. *Journal of Statistical Software,* 34, 1-24.

Crowther, T. W., Maynard, D. S., Leff, J. W., Oldfield, E. E., McCulley, R. L., Fierer, N. and Bradford, M. A., 2014. Predicting the responsiveness of soil biodiversity to deforestation: a cross-biome study. *Global Change Biology,* 20 (9), 2983-2994.

Cumming, G. S., 2011. Spatial resilience: integrating landscape ecology, resilience, and sustainability. *Landscape Ecology*, 26 (7), 899-909.

Cumming, G.S., Olsson, P., Chapin, F.S. and Holling, C.S., 2013. Resilience, experimentation, and scale mismatches in social-ecological landscapes. *Landscape Ecology*, 28 (6), 1139-1150.

Cunniffe, N. J., Cobb, R. C., Meentemeyer, R. K., Rizzo, D. M. and Gilligan, C. A., 2016. Modeling when, where, and how to manage a forest epidemic, motivated by sudden oak death in California. *Proceedings of the National Academy of Sciences,* 113 (20), 5640-5645.

Curran, L. M., Caniago, I., Paoli, G. D., Astianti, D., Kusneti, M., Leighton, M., Nirarita, C. E. and Haeruman, H., 1999. Impact of El Nino and logging on canopy tree recruitment in Borneo. *Science,* 286 (5447), 2184-2188.

Dai, L., Vorselen, D., Korolev, K. S. and Gore, J., 2012. Generic indicators for loss of resilience before a tipping point leading to population collapse. *Science,* 336 (6085), 1175-1177.

Dakos, V., Scheffer, M., van Nes, E. H., Brovkin, V., Petoukhov, V. and Held, H., 2008. Slowing down as an early warning signal for abrupt climate change. *Proceedings of the National Academy of Sciences,* 105 (38), 14308-14312.

Dale, V. H., Joyce, L. A., McNulty, S., Neilson, R. P., Ayres, M. P., Flannigan, M. D., Hanson, P. J., Irland, L. C., Lugo, A. E., Peterson, C. J., Simberloff, D., Swanson, F. J., Stocks, B. J. and Wotton, B. M., 2001. Climate change and forest disturbances: climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. *BioScience,* 51 (9), 723-734.

Davies, H., Brereton, T. M., Roy, D. B. and Fox, R., 2007. Government targets for protected area management: will threatened butterflies benefit? *Biodiversity and Conservation,* 16 (13), 3719-3736.

de Filho, F. J. B. O. and Metzger, J. P., 2006. Thresholds in landscape structure for three common deforestation patterns in the Brazilian Amazon. *Landscape Ecology,* 21 (7), 1061-1073.

de Groot, R. S., Wilson, M. A. and Boumans, R. M. J., 2002. A typology for the classification, description and valuation of ecosystem functions, goods and services. *Ecological Economics,* 41 (3), 393-408.

de Vries, F. T., Thébault, E., Liiri, M., Birkhofer, K., Tsiafouli, M. A., Bjørnlund, L., Bracht Jørgensen, H., Brady, M. V., Christensen, S., de Ruiter, P. C., d'Hertefeldt, T., Frouz, J., Hedlund, K., Hemerik, L., Hol, W. H. G., Hotes, S., Mortimer, S. R., Setälä, H., Sgardelis, S. P., Uteseny, K., van der Putten, W. H., Wolters, V. and Bardgett, R. D., 2013. Soil food web properties explain ecosystem services across European land use systems. *Proceedings of the National Academy of Sciences,* 110 (35), 14296-14301.

Deangelis, D., Post, W. M. and Travis, C. C., 2012. *Positive feedback in natural systems*. Dordrecht, Netherlands: Springer Science and Business Media.
Debinski, D. M. and Holt, R. D., 2000. A survey and overview of habitat fragmentation experiments. *Conservation Biology*, 14 (2), 342-355.
Defra, 2011. *Government response to the making space for nature review*. London, UK: Defra. PB13537.
Deluca, T., Zewdie, S., Zackrisson, O., Healey, J. and Jones, D., 2013. Bracken fern (*Pteridium aquilinum* L. kuhn) promotes an open nitrogen cycle in heathland soils. *Plant and Soil*, 367 (1-2), 521-534.
DeRose, R. J. and Long, J. N., 2014. Resistance and resilience: a conceptual framework for silviculture. *Forest Science*, 60 (6), 1205-1212.
DeWalt, S. J., Maliakal, S. K. and Denslow, J. S., 2003. Changes in vegetation structure and composition along a tropical forest chronosequence: implications for wildlife. *Forest Ecology and Management*, 182 (1), 139-151.
Díaz, S., Fargione, J., Chapin III, F. S. and Tilman, D., 2006. Biodiversity loss threatens human well-being. *PLoS Biology*, 4 (8), e277.
Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B. and Collen, B., 2014. Defaunation in the Anthropocene. *Science*, 345 (6195), 401-406.
Donohue, I., Hillebrand, H., Montoya, J. M., Petchey, O. L., Pimm, S. L., Fowler, M. S., Healy, K., Jackson, A. L., Lurgi, M., McClean, D. and O'Connor, N. E., 2016.
Dormann, C. F., McPherson, J. M., Araújo, M. B., Bivand, R., Bolliger, J., Carl, G., Davies, R. G., Hirzel, A., Jetz, W., Kissling, D. W., Kühn, I., Ohlemüller, R., Peres-Neto, P. R., Reineking, B., Schröder, B., Schurr, F. M. and Wilson, R., 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography*, 30 (5), 609-628.
Navigating the complexity of ecological stability. *Ecology Letters*, 19 (9), 1172-1185.
Duffy, J. E., 2009. Why biodiversity is important to the functioning of real-world ecosystems. *Frontiers in Ecology and the Environment*, 7 (8), 437-444.
Dunne, J. A., Saleska, S. R., Fischer, M. L. and Harte, J., 2004. Integrating experimental and gradient methods in ecological climate change research. *Ecology*, 85 (4), 904-916.
Duquesnay, A., Dupouey, J. L., Clement, A., Ulrich, E. and Le Tacon, F., 2000. Spatial and temporal variability of foliar mineral concentration in beech (*Fagus sylvatica*) stands in northeastern France. *Tree Physiology*, 20 (1), 13-22.
Eberhardt, L. L., 1978. Transect methods for population studies. *The Journal of Wildlife Management*, 42 (1), 1-31.
EEA, 2002. *An inventory of biodiversity indicators in Europe* [online]. Luxembourg: The European Environment Agency. EEA Technical report No. 92. Available from: http://www.eea.europa.eu/publications/technical_report_2004_92 [Accessed Aug 2015].
EEA, 2012. *Streamlining European Biodiversity Indicators 2020: building a future on lessons learnt from the SEBI 2010 process*. Luxembourg: The European Environment Agency. EEA Technical report No. 11/2012.
EEA, 2016. *Mapping and assessing the condition of Europe's ecosystems: progress and challenges: EEA contribution to the implementation of the EU Biodiversity Strategy to 2020*. Luxembourg: Publications Office of the European Union. EEA Technical report No. 3/2016.
Ehrenfeld, J. G., Ravit, B. and Elgersma, K., 2005. Feedback in the plant-soil system. *Annual Review of Environment and Resources*, 30 (1), 75-115.
Eichhorn, J., Roskams, P., Ferretti, M., Mues, V., Szepesi, A. and Durrant, D., 2010. *Manual on methods and criteria for harmonized sampling, assessment,*

monitoring and analysis of the effects of air pollution on forests: visual assessment of crown condition and damaging agents. Manual part IV. UNECE ICP Forests Programme Co-ordinating Centre, Hamburg: UNECE ICP Forests Programme.

Eiswerth, M. E. and Haney, J. C., 2001. Maximizing conserved biodiversity: why ecosystem indicators and thresholds matter. *Ecological Economics,* 38 (2), 259-274.

Ellis, J. E. and Swift, D. M., 1988. Stability of African pastoral ecosystems: alternate paradigms and implications for development. *Journal of Range Management,* 41 (6), 450-459.

Ene, L. T., Næsset, E., Gobakken, T., Mauya, E. W., Bollandsås, O. M., Gregoire, T. G., Ståhl, G. and Zahabu, E., 2016. Large-scale estimation of aboveground biomass in Miombo woodlands using airborne laser scanning and national forest inventory data. *Remote Sensing of Environment,* 186, 626-636.

EPA, 2012. *U.S. Environmental Protection Agency Climate Change Adaption Plan. Public review draft* [online]. Available from: http://www.epa.gov/climatechange/pdfs/EPA-climate-change-adaptationplan-final-for-public-comment-2-7-13.pdf [Accessed July 2016].

Escudero, A., del Arco, J. M., Sanz, I. C. and Ayala, J., 1992. Effects of leaf longevity and retranslocation efficiency on the retention time of nutrients in the leaf biomass of different woody species. *Oecologia,* 90 (1), 80-87.

Estreguil, C., Caudullo, G. and Miguel, J. S., 2013. *Connectivity of Natura 2000 Forest Sites. Executive report* [online]. Joint Research Centre of the European Commission, Ispra, Italy: European Commission. No. JRC 83104.

European Commission, 2013. *Communication from the Commission to the European Parliament, the Council, the European Economic and Social Committee and the Committee of the Regions. Green Infrastructure (GI) — Enhancing Europe's Natural Capital* [Online]. Brussels: European Commission. Available from: http://eur-lex.europa.eu/resource.html?uri=cellar:d41348f2-01d5-4abe-b817-4c73e6f1b2df.0014.03/DOC_1andformat=PDF [Accessed May 2013].

Fahrig, L., 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis. *Ecological Applications,* 12 (2), 346-353.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34 (1), 487-515.

Fahrig, L., 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography,* 40 (9), 1649-1663.

Fahy, O. and Gormally, M., 1998. A comparison of plant and carabid beetle communities in an Irish oak woodland with a nearby conifer plantation and clearfelled site. *Forest Ecology and Management*, 110 (1), 263-273.

Failing, L. and Gregory, R., 2003. Ten common mistakes in designing biodiversity indicators for forest policy. *Journal of Environmental Management*, 68 (2), 121-132.

Falcone, J. A., Carlisle, D. M., Weber, L. C., 2010. Quantifying human disturbance in watersheds: variable selection and performance of a GIS-based disturbance index for predicting the biological condition of perennial streams. *Ecological Indicators*, 10, 264–273.

Farley, J. and Voinov, A., 2016. Economics, socio-ecological resilience and ecosystem services. *Journal of Environmental Management,* 183, 389-398.

Fearnside, P. M., 2005. Deforestation in Brazilian Amazonia: history, rates, and consequences. *Conservation Biology,* 19 (3), 680-688.

Fedrowitz, K., Kuusinen, M. and Snäll, T., 2012. Metapopulation dynamics and future persistence of epiphytic cyanolichens in a European boreal forest ecosystem. *Journal of Applied Ecology,* 49 (2), 493-502.
Fennessy, M. S., Jacobs, A. D. and Kentula, M. E., 2007. An evaluation of rapid methods for assessing the ecological condition of wetlands. *Wetlands,* 27 (3), 543-560.
Fergnani, P. N., Sackmann, P. and Ruggiero, A., 2010. Richness-environment relationships in epigaeic ants across the Subantarctic-Patagonian transition zone. *Insect Conservation and Diversity,* 3 (4), 278-290.
Ferrari, S. and Cribari-Neto, F., 2004. Beta regression for modelling rates and proportions. *Journal of Applied Statistics,* 31 (7), 799-815.
Ferraro, P. J. and Hanauer, M. M., 2014. Quantifying causal mechanisms to determine how protected areas affect poverty through changes in ecosystem services and infrastructure. *Proceedings of the National Academy of Sciences,* 111 (11), 4332-4337.
Ferris, R. and Humphrey, J. W., 1999. A review of potential biodiversity indicators for application in British forests. *Forestry,* 72 (4), 313-328.
Filotas, E., Parrott, L., Burton, P. J., Chazdon, R. L., Coates, K. D., Coll, L., Haeussler, S., Martin, K., Nocentini, S., Puettmann, K. J., Putz, F. E., Simard, S. W. and Messier, C., 2014. Viewing forests through the lens of complex systems science. *Ecosphere,* 5 (1), 1-23.
Finegan, B., 1984. Forest succession. *Nature*, 312 (8), 109-114.
Fischer, R. and Lorenz, M., 2011. *Forest condition in Europe: 2011 technical report of ICP Forests and FutMon* [online]. Hamburg, Germany: Institute for World Forestry. 2011/1.
Fisher, B., Turner, R. K. and Morling, P., 2009. Defining and classifying ecosystem services for decision making. *Ecological Economics,* 68 (3), 643-653.
Fisichelli, N. A., Frelich, L. E. and Reich, P. B., 2014. Temperate tree expansion into adjacent boreal forest patches facilitated by warmer temperatures. *Ecography,* 37 (2), 152-161.
Flather, C. H. and Bevers, M., 2002. Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. *The American Naturalist,* 159 (1), 40-56.
Flower, C.E. and Gonzalez-Meler, M.A., 2015. Responses of temperate forest productivity to insect and pathogen disturbances. *Annual Review of Plant Biology*, 66, 547-569.
Flowers, N. and Tubbs, C. R., 1982. *The New Forest, Hampshire: Management proposals for the un-enclosed woodlands and woodlands of special importance in the Statutory Inclosures.* Peterborough, UK: Nature Conservancy Council.
Foley, J. A., Asner, G. P., Costa, M. H., Coe, M. T., DeFries, R., Gibbs, H. K., Howard, E. A., Olson, S., Patz, J., Ramankutty, N. and Snyder, P., 2007. Amazonia revealed: forest degradation and loss of ecosystem goods and services in the Amazon Basin. *Frontiers in Ecology and the Environment,* 5 (1), 25-32.
Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., Gibbs, H. K., Helkowski, J. H., Holloway, T., Howard, E. A., Kucharik, C. J., Monfreda, C., Patz, J. A., Prentice, I. C., Ramankutty, N. and Snyder, P. K., 2005. Global consequences of land use. *Science,* 309 (5734), 570-574.
Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. and Holling, C., 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics*, 35, 557-581.

Ford, E. D., 2000. *Scientific method for ecological research*. Cambridge, UK: Cambridge University Press.

Forest Europe, UNECE and FAO, 2011. *State of Europe's forests 2011: Status and trends in sustainable forest management in Europe* [online]. Oslo, Norway: Ministerial Conference on the Protection of Forests in Europe.

França, F., Louzada, J., Korasaki, V., Griffiths, H., Silveira, J. M. and Barlow, J., 2016. Do space-for-time assessments underestimate the impacts of logging on tropical biodiversity? An Amazonian case study using dung beetles. *Journal of Applied Ecology,* 53 (4), 1098-1105.

Frank, D., Finckh, M. and Wirth, C., 2009. Impacts of land use on habitat functions of old-growth forests and their biodiversity. *In:* Wirth, C. Gleixner, G. and Heimann, M., eds. *Old-growth forests*. Berlin and Heidelberg, Germany: Springer, 429–450.

Frank, S., Fürst, C., Koschke, L. and Makeschin, F., 2012. A contribution towards a transfer of the ecosystem service concept to landscape planning using landscape metrics. *Ecological Indicators,* 21, 30-38.

Fuller, R. J., Oliver, T. H. and Leather, S. R., 2008. Forest management effects on carabid beetle communities in coniferous and broadleaved forests: implications for conservation. *Insect Conservation and Diversity*, 1 (4), 242-252.

Fukami, T. and Wardle, D. A., 2005. Long-term ecological dynamics: reciprocal insights from natural and anthropogenic gradients. *Proceedings of the Royal Society B: Biological Sciences,* 272 (1577), 2105-2115.

Gálhidy, L., Mihók, B., Hagyó, A., Rajkai, K. and Standovár, T., 2006. Effects of gap size and associated changes in light and soil moisture on the understorey vegetation of a Hungarian beech forest. *Plant Ecology,* 183 (1), 133-145.

Galloway, J. N., Dentener, F. J., Capone, D. G., Boyer, E. W., Howarth, R. W., Seitzinger, S. P., Asner, G. P., Cleveland, C. C., Green, P. A., Holland, E. A., Karl, D. M., Michaels, A. F., Porter, J. H., Townsend, A. R. and Vöosmarty, C. J., 2004. Nitrogen cycles: past, present, and future. *Biogeochemistry,* 70 (2), 153-226.

Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M. C., Fröberg, M., Stendahl, J., Philipson, C. D., Mikusiński, G., Andersson, E., Westerlund, B., Andrén, H., Moberg, F., Moen, J. and Bengtsson, J., 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature Communications,* 4, 1340.

Gao, T., Hedblom, M., Emilsson, T. and Nielsen, A. B., 2014. The role of forest stand structure as biodiversity indicator. *Forest Ecology and Management,* 330, 82-93.

Gao, T., Nielsen, A. B. and Hedblom, M., 2015. Reviewing the strength of evidence of biodiversity indicators for forest ecosystems in Europe. *Ecological Indicators,* 57, 420-434.

Garabedian, J. E., McGaughey, R. J., Reutebuch, S. E., Parresol, B. R., Kilgo, J. C., Moorman, C. E. and Peterson, M. N., 2014. Quantitative analysis of woodpecker habitat using high-resolution airborne lidar estimates of forest structure and composition. *Remote Sensing of Environment,* 145, 68-80.

Gaston, K. J., Charman, K., Jackson, S. F., Armsworth, P. R., Bonn, A., Briers, R. A., Callaghan, C. S. Q., Catchpole, R., Hopkins, J., Kunin, W. E., Latham, J., Opdam, P., Stoneman, R., Stroud, D. A. and Tratt, R., 2006. The ecological effectiveness of protected areas: the United Kingdom. *Biological Conservation,* 132 (1), 76-87.

Geßler, A., Keitel, C., Kreuzwieser, J., Matyssek, R., Seiler, W. and Rennenberg, H., 2007. Potential risks for European beech (*Fagus sylvatica* L.*)* in a changing climate. *Trees,* 21 (1), 1-11.

Ghebrezgabher, M. G., Yang, T., Yang, X., Wang, X. and Khan, M., 2016. Extracting and analyzing forest and woodland cover change in Eritrea based on landsat data using supervised classification. *The Egyptian Journal of Remote Sensing and Space Science,* 19 (1), 37-47.

Gibson, D. J., 2002. *Methods in comparative plant population ecology.* Oxford, UK: Oxford University Press.

Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., Peres, C. A., Bradshaw, C. J. A., Laurance, W. F., Lovejoy, T. E. and Sodhi, N. S., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature,* 478 (7369), 378-381.

Gimona, A., Poggio, L., Brown, I. and Castellazzi, M. (2012). Woodland networks in a changing climate: threats from land use change. *Biological Conservation,* 149 (1), 93-102.

Gleason, C. J. and Im, J., 2012. Forest biomass estimation from airborne lidar data using machine learning approaches. *Remote Sensing of Environment,* 125, 80-91.

Gómez-Hernández, M., Williams-Linera, G., Guevara, R. and Lodge, D. J., 2012. Patterns of macromycete community assemblage along an elevation gradient: options for fungal gradient and metacommunity analyse. *Biodiversity and Conservation,* 21 (9), 2247-2268.

Gonzalez, A., Mouquet, N. and Loreau, M., 2009. Biodiversity as spatial insurance: the effects of habitat fragmentation and dispersal on ecosystem functioning. *In:* Naeem, S., Bunker, D.E., Hector, A., Loreau, M. and Perrings, C., eds. *Biodiversity, ecosystem functioning, and human wellbeing: an ecological and economic perspective*. New York, USA: Oxford University Press, 134–146.

Goodwin, B. J., 2003. Is landscape connectivity a dependent or independent variable? *Landscape Ecology,* 18 (7), 687-699.

Grant, M. J. and Edwards, M. E., 2008. Conserving idealized landscapes: past history, public perception and future management in the New Forest (UK). *Vegetation History and Archaeobotany,* 17 (5), 551-562.

Grêt-Regamey, A., Rabe, S.-E., Crespo, R., Lautenbach, S., Ryffel, A. and Schlup, B., 2014. On the importance of non-linear relationships between landscape patterns and the sustainable provision of ecosystem services. *Landscape Ecology,* 29 (2), 201-212.

Grimm, N. B., Chapin, F. S., Bierwagen, B., Gonzalez, P., Groffman, P. M., Luo, Y., Melton, F., Nadelhoffer, K., Pairis, A., Raymond, P. A., Schimel, J. and Williamson, C. E., 2013. The impacts of climate change on ecosystem structure and function. *Frontiers in Ecology and the Environment,* 11 (9), 474-482.

Grimm, V. and Wissel, C., 1997. Babel, or the ecological stability discussions: An inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia,* 109 (3), 323-334.

Grman, E., Lau, J. A., Schoolmaster, D. R. and Gross, K. L., 2010. Mechanisms contributing to stability in ecosystem function depend on the environmental context. *Ecology Letters,* 13 (11), 1400-1410.

Groffman, P. M., Baron, J. S., Blett, T., Gold, A. J., Goodman, I., Gunderson, L. H., Levinson, B. M., Palmer, M. A., Paerl, H. W. and Peterson, G. D., 2006. Ecological thresholds: the key to successful environmental management or an important concept with no practical application? *Ecosystems,* 9 (1), 1-13.

Grossiord, C., Granier, A., Gessler, A., Jucker, T. and Bonal, D., 2014. Does drought influence the relationship between biodiversity and ecosystem functioning in boreal forests? *Ecosystems,* 17 (3), 394-404.

Gunderson, L. and Light, S. S., 2006. Adaptive management and adaptive governance in the everglades ecosystem. *Policy Sciences,* 39 (4), 323-334.

Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E., Sexton, J. O., Austin, M. P. and Collins, C. D., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances,* 1 (2), e1500052.

Haddad, N. M., Gonzalez, A., Brudvig, L. A., Burt, M. A., Levey, D. J. and Damschen, E. I., 2017. Experimental evidence does not support the Habitat Amount Hypothesis. *Ecography,* 40 (1), 48-55.

Hagan, J. M. and Whitman, A. A., 2006. Biodiversity indicators for sustainable forestry: simplifying complexity. *Journal of Forestry,* 104 (4), 203-210.

Hajabbasi, M. A., Jalalian, A. and Karimzadeh, H. R., 1997. Deforestation effects on soil physical and chemical properties, Lordegan, Iran. *Plant and Soil,* 190 (2), 301-308.

Haines-Young, R. and Potschin, M., 2008. *England's terrestrial ecosystem services and the rationale for an ecosystem approach.* Overview Report, Defra Project Code NR0107.

Hamburg, S. P., Yanai, R. D., Arthur, M. A., Blum, J. D. and Siccama, T. G., 2003. Biotic control of calcium cycling in northern hardwood forests: acid rain and aging forests. *Ecosystems,* 6 (4), 399-406.

Hannah, L., Carr, J. L. and Lankerani, A., 1995. Human disturbance and natural habitat: a biome level analysis of a global data set. *Biodiversity and Conservation,* 4 (2), 128-155.

Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S. J., Loveland, T. R., Kommareddy, A., Egorov, A., Chini, L., Justice, C. O. and Townshend, J. R. G., 2013. High-resolution global maps of 21st-century forest cover change. *Science,* 342 (6160), 850-853.

Hansen, M. C., Stehman, S. V. and Potapov, P. V., 2010. Quantification of global gross forest cover loss. *Proceedings of the National Academy of Sciences,* 107 (19), 8650-8655.

Haque, S. S., Gupta, S. D. and Miah, S., 2014. Deforestation effects on biological and other important soil properties in an upland watershed of Bangladesh. *Journal of Forestry Research,* 25 (4), 877-885.

Härdtle, W., Von Oheimb, G. and Westphal, C., 2003. The effects of light and soil conditions on the species richness of the ground vegetation of deciduous forests in northern Germany (Schleswig-Holstein). *Forest Ecology and Management,* 182 (1), 327-338.

Hartmann, M., Howes, C. G., VanInsberghe, D., Yu, H., Bachar, D., Christen, R., Nilsson, R. H., Hallam, S. J. and Mohn, W. W., 2012. Significant and persistent impact of timber harvesting on soil microbial communities in Northern coniferous forests. *The ISME Journal,* 6 (12), 2199-2218.

Heffernan, J. B., Soranno, P. A., Angilletta, M. J., Buckley, L. B., Gruner, D. S., Keitt, T. H., Kellner, J. R., Kominoski, J. S., Rocha, A. V., Xiao, J., Harms, T. K., Goring, S. J., Koenig, L. E., McDowell, W. H., Powell, H., Richardson, A. D., Stow, C. A., Vargas, R. and Weathers, K. C., 2014. Macrosystems ecology: understanding ecological patterns and processes at continental scales. *Frontiers in Ecology and the Environment,* 12 (1), 5-14.

Heilmann-Clausen, J., Aude, E., van Dort, K., Christensen, M., Piltaver, A., Veerkamp, M., Walleyn, R., Siller, I., Standovár, T. and Òdor, P., 2014. Communities of wood-inhabiting bryophytes and fungi on dead beech logs in Europe – reflecting substrate quality or shaped by climate and forest conditions? *Journal of Biogeography,* 41 (12), 2269-2282.

Heller, N. E. and Zavaleta, E. S., 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biological Conservation,* 142 (1), 14-32.
Hermy, M. and Verheyen, K., 2007. Legacies of the past in the present-day forest biodiversity: A review of past land-use effects on forest plant species composition and diversity. *Ecological Research,* 22 (3), 361-371.
Herrault, P.-A., Larrieu, L., Cordier, S., Gimmi, U., Lachat, T., Ouin, A., Sarthou, J.-P. and Sheeren, D., 2016. Combined effects of area, connectivity, history and structural heterogeneity of woodlands on the species richness of hoverflies (diptera: Syrphidae). *Landscape Ecology,* 31 (4), 877-893.
Hicke, J.A., Allen, C.D., Desai, A.R., Dietze, M.C., Hall, R.J., Kashian, D.M., Moore, D., Raffa, K.F., Sturrock, R.N. and Vogelmann, J., 2012. Effects of biotic disturbances on forest carbon cycling in the United States and Canada. *Global Change Biology,* 18 (1), 7-34.
Higgins, M. A., Asner, G. P., Anderson, C. B., Martin, R. E., Knapp, D. E., Tupayachi, R., Perez, E., Elespuru, N. and Alonso, A., 2015. Regional-scale drivers of forest structure and function in northwestern Amazonia. *PLoS ONE,* 10 (3), e0119887.
Hill, M. O., Preston, C. D. and Roy, D., 2004. *PLANTATT. Attributes of British and Irish plants: status, size, life history, geography and habitats* [online]. Cambridge, UK: NERC Centre for Ecology and Hydrology. Available from: http://nora.nerc.ac.uk/9535/1/PLANTATT.pdf [Accessed March 2016].
Hill, R. and Hinsley, S., 2015. Airborne lidar for woodland habitat quality monitoring: exploring the significance of lidar data characteristics when modelling organism-habitat relationships. *Remote Sensing,* 7 (4), 3446.
Hill, R. A., Hinsley, S. A. and Broughton, R. K., 2014. Assessing habitats and organism-habitat relationships by airborne laser scanning. *In:* Maltamo, M., Næsset, E. and Vauhkonen, J., eds. *Forestry applications of airborne laser scanning: concepts and case studies*. Dordrecht: Springer Netherlands, 335-356.
Hinsley, S. A., Hill, R. A., Bellamy, P., Broughton, R. K., Harrison, N. M., Mackenzie, J. A., Speakman, J. R. and Ferns, P. N., 2009. Do highly modified landscapes favour generalists at the expense of specialists? An example using woodland birds. *Landscape Research,* 34 (5), 509-526.
Hirota, M., Holmgren, M., van Nes, E. H. and Scheffer, M., 2011. Global resilience of tropical forest and savanna to critical transitions. *Science,* 334 (6053), 232-235.
HM Government, 2011. *The natural choice: securing the value of nature* [online]. London, UK: HMSO. Available from: https://www.gov.uk/government/uploads/system/uploads/attachment_data/file/228842/8082.pdf [Accessed June 2015].
Hobi, M. L., Commarmot, B. and Bugmann, H., 2015. Pattern and process in the largest primeval beech forest of Europe (Ukrainian Carpathians). *Journal of Vegetation Science,* 26 (2), 323-336.
Hockings, M., 2003. Systems for assessing the effectiveness of management in protected areas. *BioScience,* 53 (9), 823-832.
Hodgson, D., McDonald, J. L. and Hosken, D. J., 2015. What do you mean, 'resilient'? *Trends in Ecology and Evolution,* 30 (9), 503-506.
Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., Harvell, C. D., Sale, P. F., Edwards, A. J., Caldeira, K., Knowlton, N., Eakin, C. M., Iglesias-Prieto, R., Muthiga, N., Bradbury, R. H., Dubi, A. and Hatziolos, M. E., 2007. Coral reefs under rapid climate change and ocean acidification. *Science,* 318 (5857), 1737-1742.
Holden, S. R. and Treseder, K. K., 2013. A meta-analysis of soil microbial biomass responses to forest disturbances [online]. *Frontiers in Microbiology,* 4, 163.

Holling, C. S., 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics,* 4 (1), 1-23.
Holling, C. S., 1978. *Adaptive environmental assessment and management.* London, UK: Wiley.
Holling, C. S., 1996a. Surprise for science, resilience for ecosystems, and incentives for people. *Ecological Applications,* 6 (3), 733-735.
Holling, C. S., 1996b. Engineering resilience versus ecological resilience. *In:* Schulze, P. C., ed. *Engineering within ecological constraints.* Washington, D. C., USA: National Academies Press, 31-44.
Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E. K., Hungate, B. A., Matulich, K. L., Gonzalez, A., Duffy, J. E., Gamfeldt, L. and O'Connor, M. I., 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature,* 486 (7401), 105-108.
Hooper, D. U., Chapin III, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J. and Wardle, D. A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs,* 75 (1), 3-35.
Huggett, A. J., 2005. The concept and utility of 'ecological thresholds' in biodiversity conservation. *Biological Conservation,* 124 (3), 301-310.
Hughes, T. P., Graham, N. A., Jackson, J. B., Mumby, P. J. and Steneck, R. S., 2010. Rising to the challenge of sustaining coral reef resilience. *Trends in Ecology and Evolution,* 25 (11), 633-642.
Humphrey, J. W., Davey, S., Peace, A. J., Ferris, R. and Harding, K., 2002. Lichens and bryophyte communities of planted and semi-natural forests in Britain: the influence of site type, stand structure and dead wood. *Biological Conservation,* 107 (2), 165-180.
Humphrey, J. W., Watts, K., Fuentes-Montemayor, E., Macgregor, N. A., Peace, A. J. and Park, K. J., 2015. What can studies of woodland fragmentation and creation tell us about ecological networks? A literature review and synthesis. *Landscape Ecology,* 30 (1), 21-50.
Huntingford, C., Fisher, R. A., Mercado, L., Booth, B. B. B., Sitch, S., Harris, P. P., Cox, P. M., Jones, C. D., Betts, R. A., Malhi, Y., Harris, G. R., Collins, M. and Moorcroft, P., 2008. Towards quantifying uncertainty in predictions of Amazon 'dieback'. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 363 (1498), 1857-1864.
Hyman, J. B. and Leibowitz, S. G., 2001. JSEM: a framework for identifying and evaluating indicators. *Environmental Monitoring and Assessment,* 66 (3), 207-232.
INPE, 2005. Monitoramento de Queimadas. Available from: https://queimadas.dgi.inpe.br/queimadas.
IPCC, 2014. *Climate change 2014: synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the intergovernmental panel on climate change.* Geneva, Switzerland: IPCC.
Isbell, F., Tilman, D., Polasky, S. and Loreau, M., 2015. The biodiversity-dependent ecosystem service debt. *Ecology Letters,* 18 (2), 119-134.
Ishii, H., Yoshimura, K.-I. and Mori, A., 2009. Convergence of leaf display and photosynthetic characteristics of understory *abies amabilis* and *tsuga heterophylla* in an old-growth forest in southwestern Washington state, USA. *Tree Physiology,* 29 (8), 989-998.
IUCN, 1994. *Guidelines for protected area management categories.* Gland and Cambridge, UK: IUCN.

Jabin, M., Mohr, D., Kappes, H. and Topp, W., 2004. Influence of dead wood on density of soil macro-arthropods in a managed oak–beech forest. *Forest Ecology and Management,* 194 (1–3), 61-69.
Jackman, S., 2015. *Package 'pscl'* [online]. R package version 1.4.9. Available from: https://cran.r-project.org/web/packages/pscl/pscl.pdf [Accessed July 2016].
Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., Cooke, R., Erlandson, J., Estes, J. A., Hughes, T. P., Kidwell, S., Lange, C. B., Lenihan, H. S., Pandolfi, J. M., Peterson, C. H., Steneck, R. S., Tegner, M. J. and Warner, R. R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science,* 293 (5530), 629-637.
Jackson, N. D. and Fahrig, L., 2016. Habitat amount, not habitat configuration, best predicts population genetic structure in fragmented landscapes. *Landscape Ecology,* 31 (5), 951-968.
Jackson, S. F. and Gaston, K. J., 2008. The unpredictability of favourability: condition assessment and protected areas in England. *Biodiversity and Conservation,* 17 (4), 749-764.
Jactel, H. and Brockerhoff, E. G., 2007. Tree diversity reduces herbivory by forest insects. *Ecology Letters,* 10 (9), 835-848.
Jakobsson, S., Fukamachi, K. and Cousins, S. A., 2016. Connectivity and management enables fast recovery of plant diversity in new linear grassland elements. *Journal of Vegetation Science*, 27 (1), 19-28.
Jenkins, K. J. and Manly, B., 2008. A double-observer method for reducing bias in faecal pellet surveys of forest ungulates. *Journal of Applied Ecology,* 45 (5), 1339-1348.
Jenkins, T. A. R., Mackie, E. D., Matthews, R. W., Miller, G., Randle, T. J. and White, M. E., 2011. *FC woodland carbon code: carbon assessment protocol.* Edinburgh, UK: Forestry Commission.
Jennings, S. B., Brown, N. D. and Sheil, D., 1999. Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. *Forestry: An International Journal of Forest Research,* 72 (1), 59-74.
JNCC, 1998. *Statement on Common Standards Monitoring (CSM)* [online]. Available from: http://jncc.defra.gov.uk/page-2198 [Accessed September 2016].
JNCC, 2003. *Guidance for Common Standards Monitoring introduction text* [online]. Peterborough, UK: Joint Nature Conservation Committee. Available from: http://jncc.defra.gov.uk/pdf/CSM_introduction.pdf [Accessed September 2016].
JNCC, 2004. *Common Standards Monitoring guidance for woodland habitats*. Peterborough, UK: Joint Nature Conservancy Committee.
JNCC, 2011. *The New Forest* [online]. Peterborough, UK: Joint Nature Conservancy Committee. Available from: http://jncc.defra.gov.uk/protectedsites/sacselection/sac.asp?EUCode=UK0012557 [Accessed March 2016].
JNCC, 2012. *Developing UK indicators for the strategic plan for biodiversity 2011-2020: habitat connectivity indicator options paper.* Peterborough, UK: Joint Nature Conservancy Committee.
Johnson, E. A. and Miyanishi, K., 2008. Testing the assumptions of chronosequences in succession. *Ecology Letters,* 11 (5), 419-431.
Jones, H. G. and Vaughan., R. A., 2010. *Remote sensing of vegetation: principles, techniques and applications.* Oxford, UK: Oxford University Press.
Jonsson, M. and Wardle, D. A., 2009. Structural equation modelling reveals plant-community drivers of carbon storage in boreal forest ecosystems [online]. *Biology Letters*, rsbl20090613.

Jouquet, P., Dauber, J., Lagerlöf, J., Lavelle, P. and Lepage, M., 2006. Soil invertebrates as ecosystem engineers: intended and accidental effects on soil and feedback loops. *Applied Soil Ecology*, 32 (2),153-164.

Jung, T., 2009. Beech decline in Central Europe driven by the interaction between *Phytophthora* infections and climatic extremes. *Forest Pathology*, 39 (2), 73-94.

Kauffman SA. 1993. *Origins of order: self-organization and selection in evolution*. Oxford, UK: Oxford University Press.

Kaye, J. P. and Hart, S. C., 1998. Restoration and canopy-type effects on soil respiration in a ponderosa pine-bunchgrass ecosystem. *Soil Science Society of America Journal*, 62 (4), 1062-1072.

Keith, D. A., Rodríguez, J. P., Rodríguez-Clark, K. M., Nicholson, E., Aapala, K., Alonso, A., Asmussen, M., Bachman, S., Basset, A., Barrow, E. G., Benson, J. S., Bishop, M. J., Bonifacio, R., Brooks, T. M., Burgman, M. A., Comer, P., Comín, F. A., Essl, F., Faber-Langendoen, D., Fairweather, P. G., Holdaway, R. J., Jennings, M., Kingsford, R. T., Lester, R. E., Nally, R. M., McCarthy, M. A., Moat, J., Oliveira-Miranda, M. A., Pisanu, P., Poulin, B., Regan, T. J., Riecken, U., Spalding, M. D. and Zambrano-Martínez, S., 2013. Scientific foundations for an IUCN red list of ecosystems. *PLoS ONE*, 8 (5), e62111.

Keith, H., Lindenmayer, D., Mackey, B., Blair, D., Carter, L., McBurney, L., Okada, S. and Konishi-Nagano, T., 2014. Managing temperate forests for carbon storage: impacts of logging versus forest protection on carbon stocks. *Ecosphere*, 5 (6), 1-34.

Kerr, J. T. and Ostrovsky, M., 2003. From space to species: ecological applications for remote sensing. *Trends in Ecology and Evolution*, 18 (6), 299-305.

Kindlmann, P. and Burel, F., 2008. Connectivity measures: a review. *Landscape Ecology*, 23 (8), 879-890.

Kint, V., Aertsen, W., Campioli, M., Vansteenkiste, D., Delcloo, A. and Muys, B., 2012. Radial growth change of temperate tree species in response to altered regional climate and air quality in the period 1901–2008. *Climatic Change*, 115 (2), 343-363.

Kinzig, A., Ryan, P., Etienne, M., Allison, H., Elmqvist, T. and Walker, B., 2006. Resilience and regime shifts: assessing cascading effects. *Ecology and Society* [online], 11 (1), 20. Available from: http://www.ecologyand society.org/vol11/iss1/art20 [Accessed February 2015].

Kirby, K. J., 2001. The impact of deer on the ground flora of British broadleaved woodland. *Forestry*, 74 (3), 219-229.

Kleiber, C. and Zeileis, A., 2016. *Applied econometrics with R*. New York, USA: Springer-Verlag.

Knorn, J. A. N., Kuemmerle, T., Radeloff, V. C., Keeton, W. S., Gancz, V., Biriş, I.-A., Svoboda, M., Griffiths, P., Hagatis, A. and Hostert, P., 2013. Continued loss of temperate old-growth forests in the Romanian Carpathians despite an increasing protected area network. *Environmental Conservation*, 40 (2), 182-193.

Koop, H. and Hilgen, P., 1987. Forest dynamics and regeneration mosaic shifts in unexploited beech (*Fagus sylvatica*) stands at Fontainebleau (France). *Forest Ecology and Management*, 20 (1), 135-150.

Korpela, I. S., 2008. Mapping of understory lichens with airborne discrete-return lidar data. *Remote Sensing of Environment*, 112 (10), 3891-3897.

Koschke, L., Fürst, C., Frank, S. and Makeschin, F., 2012. A multi-criteria approach for an integrated land-cover-based assessment of ecosystem services provision to support landscape planning. *Ecological Indicators*, 21, 54-66.

Kowalski, T., 2006. *Chalara fraxinea* sp. nov. associated with dieback of ash (*Fraxinus excelsior*) in Poland. *Forest Pathology*, 36 (4), 264-270.

Kurz, W. A., Dymond, C. C., Stinson, G., Rampley, G. J., Neilson, E. T., Carroll, A. L., Ebata, T. and Safranyik, L., 2008. Mountain pine beetle and forest carbon feedback to climate change. *Nature*, 452 (7190), 987-990.

La Porta, N., Capretti, P., Thomsen, I.M., Kasanen, R., Hietala, A.M. and von Weissenberg, K., 2008. Forest pathogens with higher damage potential due to climate change in Europe. *Canadian Journal of Plant Pathology*, 30 (2), 177-195.

Laliberté, E., Wells, J. A., Declerck, F., Metcalfe, D. J., Catterall, C. P., Queiroz, C., Aubin, I., Bonser, S. P., Ding, Y., Fraterrigo, J. M., McNamara, S., Morgan, J. W., Merlos, D. S., Vesk, P. A. and Mayfield, M. M., 2010. Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecology Letters*, 13, 76-86.

Lambin, E. F. and Meyfroidt, P., 2011. Global land use change, economic globalization, and the looming land scarcity. *Proceedings of the National Academy of Sciences*, 108 (9), 3465-3472.

Lanly, J.-P., 2003. *Deforestation and forest degradation factors* [online]. Quebec City, Canada: XII World Forestry Congress. Available from: http://www.fao.org/docrep/article/wfc/xii/ms12a-e.htm [Accessed February 2015].

Laurance, W. F., 1999. Reflections on the tropical deforestation crisis. *Biological Conservation*, 91 (2–3), 109-117.

Laurance, W. F., Sayer, J. and Cassman, K. G., 2014. Agricultural expansion and its impacts on tropical nature. *Trends in Ecology and Evolution*, 29 (2), 107-116.

Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P. and Rossi, J. P., 2006. Soil invertebrates and ecosystem services. *European Journal of Soil Biology*, 42 (1), 3-15.

Lavelle, P., Spain, A., Blouin, M., Brown, G., Decaëns, T., Grimaldi, M., Jiménez, J. J., McKey, D., Mathieu, J., Velasquez, E. and Zangerlé, A., 2016. Ecosystem engineers in a self-organized soil: a review of concepts and future research questions. *Soil Science*, 181 (4), 91-109.

Lavorel, S., Colloff, M. J., McIntyre, S., Doherty, M. D., Murphy, H. T., Metcalfe, D. J., Dunlop, M., Williams, R. J., Wise, R. M. and Williams, K. J., 2015. Ecological mechanisms underpinning climate adaptation services. *Global Change Biology* (21), 12–31.

Lawley, V., Lewis, M., Clarke, K. and Ostendorf, B., 2016. Site-based and remote sensing methods for monitoring indicators of vegetation condition: an Australian review. *Ecological Indicators*, 60, 1273-1283.

Lawton, J. H., Brotherton, P. N. M., Brown, V. K., Elphick, C., Fitter, A. H., Forshaw, J., Haddow, R. W., Hilborne, S., Leafe, R. N., Mace, G. M., Southgate, M. P., Sutherland, W. J., Tew, T. E., Varley, J. and Wynne, G. R., 2010. *Making space for nature: a review of England's wildlife sites and ecological network* [online]. Defra.

Legg, C. J. and Nagy, L., 2006. Why most conservation monitoring is, but need not be, a waste of time. *Journal of Environmental Management*, 78 (2), 194-199.

Leite, M. S., Tambosi, L. R., Romitelli, I. and Metzger, J. P., 2013. Landscape ecology perspective in restoration projects for biodiversity conservation: a review. *Natureza and Conservação*, 11, 108-188.

Lenton, T. M., 2011. Early warning of climate tipping points. *Nature Climate Change*, 1 (4), 201-209.

Lenton, T. M. and Williams, H. T. P., 2013. On the origin of planetary-scale tipping points. *Trends in Ecology and Evolution*, 28 (7), 380-382.

Levanoni, O., Levin, N., Pe'er, G., Turbé, A. and Kark, S., 2011. Can we predict butterfly diversity along an elevation gradient from space? *Ecography,* 34 (3), 372-383.

Leverington, F., Costa, K. L., Pavese, H., Lisle, A. and Hockings, M., 2010. A global analysis of protected area management effectiveness. *Environmental Management,* 46 (5), 685-698.

Levin, S. A., 1992. The problem of pattern and scale in ecology: The Robert H. MacArthur award lecture. *Ecology,* 73 (6), 1943-1967.

Lewontin, R. C., 1969. The meaning of stability. *Brookhaven Symposia in Biology,* 22, 13-24.

Liao, K.-H., 2012. A theory on urban resilience to floods—a basis for alternative planning practices. *Ecology and Society,* 17 (4).

Liebsch, D., Marques, M. C. and Goldenberg, R., 2008. How long does the Atlantic Rain Forest take to recover after a disturbance? Changes in species composition and ecological features during secondary succession. *Biological Conservation,* 141 (6), 1717-1725.

Liira, J. and Paal, T., 2013. Do forest-dwelling plant species disperse along landscape corridors? *Plant Ecology*, 214 (3), 455-470.

Lindenmayer, D.B. and Laurance, W.F., 2016. The unique challenges of conserving large old trees. *Trends in Ecology and Evolution*, 31 (6), 416-418.

Lindenmayer, D. and Luck, G., 2005. Synthesis: thresholds in conservation and management. *Biological Conservation,* 124 (3), 351-354.

Lindenmayer, D. B., Gibbons, P., Bourke, M., Burgman, M., Dickman, C. R., Ferrier, S., Fitzsimons, J., Freudenberger, D., Garnett, S. T., Groves, C., Hobbs, R. J., Kingsford, R. T., Krebs, C., Legge, S., Lowe, A. J., McLean, R., Montambault, J., Possingham, H., Radford, J., Robinson, D., Smallbone, L., Thomas, D., Varcoe, T., Vardon, M., Wardle, G., Woinarksi, J. and Zerger, A., 2012. Improving biodiversity monitoring. *Austral Ecology,* 37 (3), 285-294.

Lindenmayer, D., Messier, C. and Sato, C., 2016. Avoiding ecosystem collapse in managed forest ecosystems. *Frontiers in Ecology and the Environment,* 14 (10), 561-568.

Lindner, M., Fitzgerald, J. B., Zimmermann, N. E., Reyer, C., Delzon, S., van der Maaten, E., Schelhaas, M.-J., Lasch, P., Eggers, J., van der Maaten-Theunissen, M., Suckow, F., Psomas, A., Poulter, B. and Hanewinkel, M., 2014. Climate change and European forests: what do we know, what are the uncertainties, and what are the implications for forest management? *Journal of Environmental Management,* 146, 69-83.

Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P., Kolström, M., Lexer, M. J. and Marchetti, M., 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *Forest Ecology and Management,* 259 (4), 698-709.

Listopad, C. M. C. S., Masters, R. E., Drake, J., Weishampel, J. and Branquinho, C., 2015. Structural diversity indices based on airborne lidar as ecological indicators for managing highly dynamic landscapes. *Ecological Indicators,* 57, 268-279.

Lopatin, J., Dolos, K., Hernández, H. J., Galleguillos, M. and Fassnacht, F. E., 2016. Comparing generalized linear models and random forest to model vascular plant species richness using lidar data in a natural forest in central Chile. *Remote Sensing of Environment,* 173, 200-210.

Loreau, M., Mouquet, N. and Gonzalez, A., 2003. Biodiversity as spatial insurance in heterogeneous landscapes. *Proceedings of the National Academy of Sciences,* 100 (22), 12765-12770.

Loudermilk, E. L., Scheller, R. M., Weisberg, P. J., Yang, J., Dilts, T. E., Karam, S. L. and Skinner, C., 2013. Carbon dynamics in the future forest: the importance of long-term successional legacy and climate–fire interactions. *Global Change Biology*, 19 (11), 3502-3515.

Lucash, M. S., Scheller, R. M., Kretchun, A. M., Clark, K. L. and Hom, J., 2014. Impacts of fire and climate change on long-term nitrogen availability and forest productivity in the new jersey pine barrens. *Canadian Journal of Forest Research*, 44 (5), 404-412.

Luo, Y., Su, B., Currie, W. S., Dukes, J. S., Finzi, A., Hartwig, U., Hungate, B., McMurtrie, R. E., Oren, R., Parton, W. J., Pataki, D. E., Shaw, R. M., Zak, D. R. and Field, C. B., 2004. Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience*, 54 (8), 731-739.

MacDougall, A.S. and Turkington, R., 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology*, 86 (1), 42-55.

Mace, G. M., Norris, K. and Fitter, A. H., 2012. Biodiversity and ecosystem services: a multilayered relationship. *Trends in Ecology and Evolution*, 27 (1), 19-26.

Mace, G. M., Reyers, B., Alkemade, R., Biggs, R., Chapin, F. S., Cornell, S. E., Díaz, S., Jennings, S., Leadley, P., Mumby, P. J. and Purvis, A., 2014. Approaches to defining a planetary boundary for biodiversity. *Global Environmental Change*, 28, 289-297.

Malhi, Y., Roberts, J. T., Betts, R. A., Killeen, T. J., Li, W. and Nobre, C. A., 2008. Climate change, deforestation, and the fate of the amazon. *Science*, 319 (5860), 169-172.

Mallik, A. U., 1995. Conversion of temperate forests into heaths: role of ecosystem disturbance and ericaceous plants. *Environmental Management*, 19 (5), 675-684.

Maltamo, M., Packalén, P., Yu, X., Eerikäinen, K., Hyyppä, J. and Pitkänen, J., 2005. Identifying and quantifying structural characteristics of heterogeneous boreal forests using laser scanner data. *Forest Ecology and Management*, 216 (1–3), 41-50.

Manners, J. and Edwards, P., 1986. Death of old beech trees in the New Forest. *Proceedings of the Hampshire Field Club and Archaeological Society*, 42, 155-156.

Martin, P. A., Newton, A. C., Cantarello, E. and Evans, P., 2015. Stand dieback and collapse in a temperate forest and its impact on forest structure and biodiversity. *Forest Ecology and Management*, 358, 130-138.

Martin, P. A., Newton, A. C., Cantarello, E. and Evans, P. M., 2017. Analysis of ecological thresholds in a temperate forest undergoing dieback. *In press*.

Maxim, L., Spangenberg, J. H. and O'Connor, M., 2009. An analysis of risks for biodiversity under the DPSIR framework. *Ecological Economics*, 69 (1), 12-23.

McCarthy, J., 2001. Gap dynamics of forest trees: a review with particular attention to boreal forests. *Environmental Reviews*, 9 (1), 1-59.

McClanahan, T. R., Graham, N. a. J., MacNeil, M. A., Muthiga, N. A., Cinner, J. E., Bruggemann, J. H. and Wilson, S. K., 2011. Critical thresholds and tangible targets for ecosystem-based management of coral reef fisheries. *Proceedings of the National Academy of Sciences*, 108 (41), 17230-17233.

McElhinny, C., Gibbons, P., Brack, C. and Bauhus, J., 2005. Forest and woodland stand structural complexity: its definition and measurement. *Forest Ecology and Management*, 218 (1–3), 1-24.

McFadden, D., 1973. Conditional logit analysis of qualitative choice behavior. *In:* Zarembka, P., ed. *Frontiers of Econometrics.* New York, UK: Academic Press, 105-142.

McGarigal, K., 2015. *Fragstats help* [online]. Amherst: University of Massachusetts. Available from: https://www.umass.edu/landeco/research/fragstats/documents/fragstats.help.4.2.pdf [Accessed September 2015].

McGee, G. G., Leopold, D. J. and Nyland, R. D., 1999. Structural characteristics of old-growth, maturing, and partially cut northern hardwood forests. *Ecological Applications,* 9 (4), 1316-1329.

MEA, 2005. *Millennium Ecosystem Assessment: Ecosystems and human well-being* [online]. Washington, D. C., USA: Island Press.

Mediavilla, S. and Escudero, A., 2003. Leaf life span differs from retention time of biomass and nutrients in the crowns of evergreen species. *Functional Ecology,* 17 (4), 541-548.

Meentemeyer, R., Rizzo, D., Mark, W. and Lotz, E., 2004. Mapping the risk of establishment and spread of sudden oak death in California. *Forest Ecology and Management,* 200 (1), 195-214.

Melo, F. P. L., Arroyo-Rodríguez, V., Fahrig, L., Martínez-Ramos, M. and Tabarelli, M., 2013. On the hope for biodiversity-friendly tropical landscapes. *Trends in Ecology and Evolution,* 28 (8), 462-468.

Messier, C., Puettmann, K., Chazdon, R., Andersson, K. P., Angers, V. A., Brotons, L., Filotas, E., Tittler, R., Parrott, L. and Levin, S. A., 2015. From management to stewardship: viewing forests as complex adaptive systems in an uncertain world. *Conservation Letters,* 8 (5), 368-377.

Mesquita, R. C., Ickes, K., Ganade, G. and Williamson, G. B., 2001. Alternative successional pathways in the Amazon Basin. *Journal of Ecology,* 89 (4), 528-537.

Met Office, 2015. *Lyndhurst climate*. Available from: http://www.metoffice.gov.uk/public/weather/climate/gcnckhuz6 [Accessed October 2015].

Michel A. K., and Seidling W., 2016. *Forest condition in Europe: 2016 technical report of ICP Forests. Report under the UNECE convention on long-range transboundary air pollution (CLRTAP).* Vienna: BFW Austrian Research Centre for Forests. BFW Dokumentation 23/2016.

Milad, M., Schaich, H., Bürgi, M. and Konold, W., 2011. Climate change and nature conservation in Central European forests: a review of consequences, concepts and challenges. *Forest Ecology and Management,* 261 (4), 829-843.

Millar, C. I. and Stephenson, N. L., 2015. Temperate forest health in an era of emerging megadisturbance. *Science,* 349 (6250), 823-826.

Millar, C. I., Stephenson, N. L. and Stephens, S. L., 2007. Climate change and forests of the future: managing in the face of uncertainty. *Ecological Applications,* 17 (8), 2145-2151.

Mitchell, M. G., Bennett, E. M. and Gonzalez, A., 2013. Linking landscape connectivity and ecosystem service provision: current knowledge and research gaps. *Ecosystems,* 16 (5), 894-908.

Mitchell, M. G. E., Suarez-Castro, A. F., Martinez-Harms, M., Maron, M., McAlpine, C., Gaston, K. J., Johansen, K. and Rhodes, J. R., 2015. Reframing landscape fragmentation's effects on ecosystem services. *Trends in Ecology and Evolution,* 30 (4), 190-198.

Mitchell, R. J., Bailey, S., Beaton, J. K., Bellamy, P. E., Brooker, R. W., Broome, A., Chetcuti, J., Eaton, S., Ellis, C. J., Farren, J., Gimona, A., Goldberg, E., Hall, J., Harmer, R., Hester, A. J., Hewison, R. L., Hodgetts, N. G., Hooper, R. J., Howe, L., Iason, G. R., Kerr, G., Littlewood, N. A., Morgan, V., Newey, S., Potts, J. M., Pozsgai, G., Ray, D., Sim, D. A., Stockan, J. A., Taylor, A. F. S. &

Woodward, S. 2014. *The potential ecological impact of ash dieback in the UK*. Peterborough, UK: JNCC. JNCC Report No. 483.
Moran, M. D., 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos*, 100 (2), 403-405.
Moran, N., Nieland, S., Tintrup, G. G., Suntrup, G. and Kleinschmit, B., 2017. Combining machine learning and ontological data handling for multi-source classification of nature conservation areas. *International Journal of Applied Earth Observation and Geoinformation*, 54, 124-133.
Mori, A. S., Shiono, T., Koide, D., Kitagawa, R., Ota, A. T. and Mizumachi, E., 2013. Community assembly processes shape an altitudinal gradient of forest biodiversity. *Global Ecology and Biogeography*, 22 (7), 878-888.
Morin, X., Fahse, L., Scherer-Lorenzen, M. and Bugmann, H., 2011. Tree species richness promotes productivity in temperate forests through strong complementarity between species. *Ecology Letters*, 14 (12), 1211-1219.
Moritz, C. and Agudo, R., 2013. The future of species under climate change: resilience or decline? *Science*, 341 (6145), 504-508.
Moritz, M. A., Parisien, M.-A., Batllori, E., Krawchuk, M. A., van Dorn, J., Ganz, D. J. and Hayhoe, K., 2012. Climate change and disruptions to global fire activity. *Ecosphere*, 3 (6), 1-22.
Morsdorf, F., Meier, E., Kötz, B., Itten, K. I., Dobbertin, M. and Allgöwer, B., 2004. Lidar-based geometric reconstruction of boreal type forest stands at single tree level for forest and wildland fire management. *Remote Sensing of Environment*, 92 (3), 353-362.
Mouillot, D., Graham, N. A., Villéger, S., Mason, N. W. and Bellwood, D. R., 2013. A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution*, 28 (3), 167-177.
Mountford, E. P. and Peterken, G. F., 2003. Long-term change and implications for the management of wood-pastures: experience over 40 years from Denny Wood, New Forest. *Forestry*, 76 (1), 19-43.
Mountford, E. P., Peterken, G. F., Edwards, P. J. and Manners, J. G., 1999. Long-term change in growth, mortality and regeneration of trees in Denny Wood, an old-growth wood-pasture in the New Forest (UK). *Perspectives in Plant Ecology, Evolution and Systematics*, 2 (2), 223-272.
Müller, F., Bergmann, M., Dannowski, R., Dippner, J. W., Gnauck, A., Haase, P., Jochimsen, M. C., Kasprzak, P., Kröncke, I., Kümmerlin, R., Küster, M., Lischeid, G., Meesenburg, H., Merz, C., Millat, G., Müller, J., Padisák, J., Schimming, C. G., Schubert, H., Schult, M., Selmeczy, G., Shatwell, T., Stoll, S., Schwabe, M., Soltwedel, T., Straile, D. and Theuerkauf, M., 2016. Assessing resilience in long-term ecological data sets. *Ecological Indicators*, 65, 10-43.
Müller, J. and Brandl, R., 2009. Assessing biodiversity by remote sensing in mountainous terrain: the potential of lidar to predict forest beetle assemblages. *Journal of Applied Ecology*, 46 (4), 897-905.
Müller-Using, S. and Bartsch, N., 2009. Decay dynamic of coarse and fine woody debris of a beech (*Fagus sylvatica* L.) forest in central Germany. *European Journal of Forest Research*, 128 (3), 287-296.
Mumby, P. J., 2009. Phase shifts and the stability of macroalgal communities on Caribbean coral reefs. *Coral Reefs*, 28 (3), 761-773.
Mumby, P. J., Hastings, A. and Edwards, H. J., 2008. Thresholds and the resilience of Caribbean coral reefs. *Nature*, 450 (7166), 98-101.
Mumby, P. J., Iglesias-Prieto, R., Hooten, A. J., Sale, P. F., Hoegh-Guldberg, O., Edwards, A. J., Harvell, C. D., Gomez, E. D., Knowlton, N. and Hatziolos, M.

E., 2011. Revisiting climate thresholds and ecosystem collapse. *Frontiers in Ecology and the Environment,* 9 (2), 94-96.
Muradian, R., 2001. Ecological thresholds: a survey. *Ecological Economics,* 38 (1), 7-24.
Murphy, B. P., Williamson, G. J. and Bowman, D. M. J. S., 2012. Did central Australian megafaunal extinction coincide with abrupt ecosystem collapse or gradual climate change? *Global Ecology and Biogeography,* 21 (2), 142-151.
Myers-Smith, I. H., Trefry, S. A. and Swarbrick, V. J., 2012. Resilience: easy to use but hard to define. *Ideas in Ecology and Evolution,* 5.
Naeem, S., Chapin Iii, F., Costanza, R., Ehrlich, P. R., Golley, F. B., Hooper, D. U., Lawton, J. H., O'Neill, R. V., Mooney, H. A. and Sala, O. E., 1999. Biodiversity and ecosystem functioning: maintaining natural life support processes. *Issues in Ecology,* 4 (11).
Nakagawa, S., 2004. A farewell to Bonferroni: the problems of low statistical power and publication bias. *Behavioral Ecology,* 15 (6), 1044-1045.
Natural England, 2013. *Natural England standard SSSI monitoring and reporting* [online]. Natural England. NESTND035.
Natural England, 2016. *Conservation 21: Natural England's conservation strategy for the 21st century* [online]. Natural England. Available from: https://www.gov.uk/government/uploads/system/uploads/attachment_data/file/562046/conservation-21.pdf [Accessed November 2016].
Natural England and RSPB, 2014. *Climate change adaptation manual: evidence to support nature conservation in a changing climate* [online]. Available from: http://publications.naturalengland.org.uk/publication/5629923804839936 [Accessed February 2016].
Nayak, P. K., Oliveira, L. E. and Berkes, F., 2014. Resource degradation, marginalization, and poverty in small-scale fisheries: Threats to social-ecological resilience in India and Brazil. *Ecology and Society,* 19.
NEA, 2011. *UK National Ecosystem Assessment: technical report.* Oxford, UK: UNEP-WCMC.
Nemec, K.T., Chan, J., Hoffman, C., Spanbauer, T.L., Hamm, J.A., Allen, C.R., Hefley, T., Pan, D. and Shrestha, P., 2014. Assessing resilience in stressed watersheds. *Ecology and Society,* 19 (1).
Neufeld, H. S. and Young, D. R., 2014. Ecophysiology of the herbaceous layer in temperate deciduous forests. *In:* Gilliam, F. S., ed. *The herbaceous layer in forests of eastern North America* 2nd ed. New York, USA: Oxford University Press, 38-90.
Newton, A. C., 2007. *Forest ecology and conservation handbook of techniques.* Cambridge, UK: Cambridge University Press.
Newton, A. C., 2010. *Biodiversity in the New Forest.* Newbury, UK: Pisces Publications.
Newton, A. C., 2016. Biodiversity risks of adopting resilience as a policy goal. *Conservation Letters,* 9 (5), 369-376.
Newton, A. C. and Cantarello, E., 2015. Restoration of forest resilience: an achievable goal? *New Forests,* 46 (5), 645-668.
Newton, A. C., Cantarello, E., Tejedor, N. and Myers, G., 2013. Dynamics and conservation management of a wooded landscape under high herbivore pressure. *International Journal of Biodiversity,* 2013, 15.
Niemeijer, D. and de Groot, R. S., 2008. A conceptual framework for selecting environmental indicator sets. *Ecological Indicators,* 8 (1), 14-25.
Niemi, G. J. and McDonald, M. E., 2004. Application of ecological indicators. *Annual Review of Ecology, Evolution, and Systematics,* 35, 89-111.

Nimmo, D. G., Mac Nally, R., Cunningham, S. C., Haslem, A. and Bennett, A. F., 2015. Vive la résistance: reviving resistance for 21st century conservation. *Trends in Ecology and Evolution*, 30 (9), 516-523.
Nordén, B. and Paltto, H., 2001. Wood-decay fungi in hazel wood: species richness correlated to stand age and dead wood features. *Biological Conservation*, 101 (1), 1-8.
Nordén, B., Dahlberg, A., Brandrud, T. E., Fritz, Ö., Ejrnaes, R. and Ovaskainen, O., 2014. Effects of ecological continuity on species richness and composition in forests and woodlands: a review. *Ecoscience*, 21 (1), 34-45
Noss, R. F., 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology*, 355-364.
Noss, R. F., 1999. Assessing and monitoring forest biodiversity: a suggested framework and indicators. *Forest Ecology and Management*, 115 (2), 135-146.
Nowak, D. J. and Dwyer, J. F., 2007. Understanding the benefits and costs of urban forest ecosystems. *In:* Kuser, J. E., ed. *Urban and community forestry in the northeast*. Dordrecht, Netherlands: Springer Netherlands, 25-46.
Ochoa-Quintero, J. M., Gardner, T. A., Rosa, I., Barros Ferraz, S. F. and Sutherland, W. J., 2015. Thresholds of species loss in Amazonian deforestation frontier landscapes. *Conservation Biology*, 29 (2), 440-451.
Olds, A. D., Pitt, K. A., Maxwell, P. S. and Connolly, R. M., 2012. Synergistic effects of reserves and connectivity on ecological resilience. *Journal of Applied Ecology*, 49 (6), 1195-1203.
Olff, H., Vera, F. W. M., Bokdam, J., Bakker, E. S., Gleichman, J. M., de Maeyer, K. and Smit, R., 1999. Shifting mosaics in grazed woodlands driven by the alternation of plant facilitation and competition. *Plant Biology*, 1 (2), 127-137.
Oliver, T. H., Brereton, T. and Roy, D. B., 2013. Population resilience to an extreme drought is influenced by habitat area and fragmentation in the local landscape. *Ecography*, 36 (5), 579-586.
Oliver, I., Eldridge, D. J., Nadolny, C. and Martin, W. K., 2014. What do site condition multi-metrics tell us about species biodiversity? *Ecological Indicators*, 38, 262-271.
Oliver, T. H., Heard, M. S., Isaac, N. J. B., Roy, D. B., Procter, D., Eigenbrod, F., Freckleton, R., Hector, A., Orme, C. D. L., Petchey, O. L., Proença, V., Raffaelli, D., Suttle, K. B., Mace, G. M., Martín-López, B., Woodcock, B. A. and Bullock, J. M., 2015. Biodiversity and resilience of ecosystem functions. *Trends in Ecology and Evolution*, 30 (11), 673-684.
Olson, M. G., Knapp, B. O. and Kabrick, J. M., 2017. Dynamics of a temperate deciduous forest under landscape-scale management: implications for adaptability to climate change. *Forest Ecology and Management*, 387, 73-85.
Olsson, L., Jerneck, A., Thoren, H., Persson, J. and O'Byrne, D., 2015. Why resilience is unappealing to social science: theoretical and empirical investigations of the scientific use of resilience. *Science Advances*, 1 (4), e1400217.
Packham, J. R., Harding, D. J. and Hilton, G. M., 2001. *Functional ecology of woodlands and forests*. Dordrecht, Netherlands: Kluwer Academic Publishers.
Packham, J. R., Thomas, P. A., Atkinson, M. D. and Degen, T., 2012. Biological flora of the British Isles: *Fagus sylvatica*. *Journal of Ecology*, 100 (6), 1557-1608.
Paillet, Y., Bergès, L., Hjältén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.-J., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., Sebastià, M.-T., Schmidt, W., Standovár, T., Tóthmérész, B., Uotila, A., Valladares, F., Vellak, K. and Virtanen, R., 2010. Biodiversity differences between managed and unmanaged

forests: meta-analysis of species richness in Europe. *Conservation Biology*, 24 (1), 101–112.
Paltto, H., Nordberg, A., Nordén, B. and Snäll, T., 2011. Development of secondary woodland in oak wood pastures reduces the richness of rare epiphytic lichens. *PLoS ONE,* 6 (9), e24675.
Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S. L., Canadell, J. G. and Ciais, P., 2011. A large and persistent carbon sink in the world's forests. *Science,* 333 (6045), 988-993.
Pardini, R., Bueno, A. D. A., Gardner, T. A., Prado, P. I. and Metzger, J. P., 2010. Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. *PLoS ONE,* 5 (10), e13666.
Parks, C. G. and Bernier, P. 2010. Adaptation of forests and forest management to changing climate with emphasis on forest health: a review of science, policies and practices. *Forest Ecology and Management*, 259, 657–659.
Parton, W. J., Anderson, D. W., Cole, C. V. and Stewart, J. W. B., 1983. Simulation of soil organic matter formation and mineralization in semiarid agroecosystems. *In:* Lowrance, R. R., Todd, R. L., Asmussen, L. E. and Leonard, R. A., eds. *Nutrient cycling in agricultural ecosystems*. Athens, Georgia, USA: The University of Georgia, College of Agriculture Experiment Stations, 533-550.
Patterson, T. M. and Coelho, D. L., 2009. Ecosystem services: foundations, opportunities, and challenges for the forest products sector. *Forest Ecology and Management,* 257 (8), 1637-1646.
Pearce, D. W.and Moran, D., 1994. *The economic value of biodiversity.* London, UK: Earthscan Publications.
Peay, K. G., Garbelotto, M. and Bruns, T .D., 2010. Evidence of dispersal limitation in soil microorganisms: isolation reduces species richness on mycorrhizal tree islands. *Ecology,* 91 (12), 3631-3640.
Peña-Claros, M., Fredericksen, T. S., Alarcón, A., Blate, G. M., Choque, U., Leaño, C., Licona, J. C., Mostacedo, B., Pariona, W., Villegas, Z. and Putz, F. E., 2008. Beyond reduced-impact logging: silvicultural treatments to increase growth rates of tropical trees. *Forest Ecology and Management*, 256 (7), 1458-1467.
Penttilä, R., Siitonen, J. and Kuusinen, M., 2004. Polypore diversity in managed and old-growth boreal *Picea abies* forests in southern Finland. *Biological Conservation,* 117 (3), 271-283.
Perakis, S. S., Sinkhorn, E. R., Catricala, C. E., Bullen, T. D., Fitzpatrick, J. A., Hynicka, J. D. and Cromack, K., 2013. Forest calcium depletion and biotic retention along a soil nitrogen gradient. *Ecological Applications,* 23 (8), 1947-1961.
Peres, C. A., Barlow, J. and Laurance, W. F., 2006. Detecting anthropogenic disturbance in tropical forests. *Trends in Ecology and Evolution,* 21 (5), 227-229.
Peringer, A., Schulze, K. A., Stupariu, I., Stupariu, M.-S., Rosenthal, G., Buttler, A. and Gillet, F., 2016. Multi-scale feedbacks between tree regeneration traits and herbivore behavior explain the structure of pasture-woodland mosaics. *Landscape Ecology,* 31 (4), 913-927.
Pessoa, M. S., Rocha-Santos, L., Talora, D. C., Faria, D., Mariano-Neto, E., Hambuckers, A. and Cazetta, E., 2017. Fruit biomass availability along a forest cover gradient. *Biotropica,* 49 (1), 45-55.
Peterken, G. F. and Lloyd, P. S., 1967. *Ilex Aquifolium* L. *Journal of Ecology,* 841-858.
Peterken, G. F. and Mountford, E. P., 1996. Effects of drought on beech in Lady Park Wood, an unmanaged mixed deciduous woodland. *Forestry: An International Journal of Forest Research*, 69 (2), 125-136.

Peterken, G. F., Spencer, J. W. and Field, A. B., 1996. *Maintaining the Ancient and Ornamental woodlands of the New Forest.* Bristol, UK: Forestry Commission.
Peterken, G. F., Spencer, J. W. and Field, A. B., 1999. *Plan for the Ancient and Ornamental woodlands of the New Forest.* Lyndhurst, UK: Forestry Commission.
Peters, R.,1997. *Beech forests*. Dordrecht, Netherlands: Kluwer.
Peters, D. P. C., Bestelmeyer, B. T. and Turner, M. G., 2007. Cross–scale interactions and changing pattern–process relationships: consequences for system dynamics. *Ecosystems,* 10 (5), 790-796.
Peterson, G., Allen, C. R. and Holling, C. S., 1998. Ecological resilience, biodiversity, and scale. *Ecosystems,* 1 (1), 6-18.
Petraitis, P., 2013. *Multiple stable states in natural ecosystems.* Oxford, UK: Oxford University Press.
Petraitis, P. S. and Hoffman, C., 2010. Multiple stable states and relationship between thresholds in processes and states. *Marine Ecology Progress Series,* 413, 189-200.
Pettorelli, N., Safi, K. and Turner, W., 2014. Satellite remote sensing, biodiversity research and conservation of the future. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 369 (1643).
Peura, M., Silveyra Gonzalez, R., Müller, J., Heurich, M., Vierling, L. A., Mönkkönen, M. and Bässler, C., 2016. Mapping a 'cryptic kingdom': performance of lidar derived environmental variables in modelling the occurrence of forest fungi. *Remote Sensing of Environment,* 186, 428-438.
Pickett, S. T. A., 1989. Space-for-time substitution as an alternative to long-term studies. *In:* Likens, G. E., ed. *Long-term studies in ecology: approaches and alternatives*. New York, USA: Springer New York, 110-135.
Pickett, S. T. A. and White, P. S., 1985. *The ecology of natural disturbance and patch dynamics.* California, USA: Academic Press.
Pimm, S. L., 1984. The complexity and stability of ecosystems. *Nature,* 307 (5949), 321-326.
Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., Raven, P. H., Roberts, C. M. and Sexton, J. O., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science,* 344 (6187).
Ponette, Q., Bispo, A., Brêthes, A., Dupouey, J. L., Feix, I., Gégout, J. C., Jabiol, B., Pousse, N. and Ranger, J., 2014. Fertility indicators in temperate forest soils: issues, approaches and prospects. *Revue Forestiere Francaise,* 66 (5), 501-515.
Porter-Bolland, L., Ellis, E. A., Guariguata, M. R., Ruiz-Mallén, I., Negrete-Yankelevich, S. and Reyes-García, V., 2012. Community managed forests and forest protected areas: an assessment of their conservation effectiveness across the tropics. *Forest Ecology and Management,* 268, 6-17.
Porporato, A., Daly, E. and Rodriguez-Iturbe, I., 2004. Soil water balance and ecosystem response to climate change. *The American Naturalist,* 164 (5), 625-632.
Post, W. M. and Pastor, J., 1996. Linkages - an individual-based forest ecosystem model. *Climatic Change,* 34 (2), 253-261.
Poulter, B., Pederson, N., Liu, H., Zhu, Z., D'Arrigo, R., Ciais, P., Davi, N., Frank, D., Leland, C., Myneni, R., Piao, S. and Wang, T., 2013. Recent trends in inner Asian forest dynamics to temperature and precipitation indicate high sensitivity to climate change. *Agricultural and Forest Meteorology,* 178–179, 31-45.
Prach, K. and Walker, L. R., 2011. Four opportunities for studies of ecological succession. *Trends in Ecology and Evolution,* 26 (3), 119-123.

Prevedello, J. A. and Vieira, M. V., 2010. Does the type of matrix matter? A quantitative review of the evidence. *Biodiversity and Conservation,* 19 (5), 1205-1223.

Pretzsch, H., Schütze, G. and Uhl, E., 2013. Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by inter-specific facilitation. *Plant Biology,* 15 (3), 483-495.

Přívětivý, T., Janík, D., Unar, P., Adam, D., Král, K. and Vrška, T., 2016. How do environmental conditions affect the dead wood decomposition of European beech (*Fagus sylvatica* L.)? *Forest Ecology and Management,* 381, 177-187.

Priwitzer, T., Capuliak, J., Bošela, M. and Schwarz, M. 2013. Preliminary results of soil respiration in beech, spruce and grassy stands, *Forestry Journal*, 59, 189-196.

Prober, S. M., Thiele, K. R. and Lunt, I. D., 2002. Identifying ecological barriers to restoration in temperate grassy woodlands: soil changes associated with different degradation states. *Australian Journal of Botany,* 50 (6), 699-712.

Putman, R. J., Edwards, P. J., Mann, J. C. E., How, R. C. and Hill, S. D., 1989. Vegetational and faunal changes in an area of heavily grazed woodland following relief of grazing. *Biological Conservation,* 47 (1), 13-32.

Pyatt, G., Spencer, J., Hutchby, L., Davani, S., Fletcher, J. and Purdy, K., 2003. *Applying the ecological site classification in the lowlands. Technical paper 33.* Edinburgh, UK: Forestry Commission.

Quinlan, A. E., Berbés-Blázquez, M., Haider, L. J. and Peterson, G. D., 2016. Measuring and assessing resilience: broadening understanding through multiple disciplinary perspectives. *Journal of Applied Ecology,* 53 (3), 677-687.

Raffa, K. F., Aukema, B. H., Bentz, B. J., Carroll, A. L., Hicke, J. A., Turner, M. G. and Romme, W. H., 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *BioScience,* 58 (6), 501-517.

Rahel, F. J., 2007. Biogeographic barriers, connectivity and homogenization of freshwater faunas: it's a small world after all. *Freshwater Biology,* 52 (4), 696-710.

Rappaport, D. I., Tambosi, L. R. and Metzger, J. P., 2015. A landscape triage approach: combining spatial and temporal dynamics to prioritize restoration and conservation. *Journal of Applied Ecology,* 52 (3), 590-601.

Reemts, C. M. and Hansen, L. L., 2008. Slow recolonization of burned oak–juniper woodlands by Ashe juniper (*Juniperus ashei*): ten years of succession after crown fire. *Forest Ecology and Management,* 255 (3–4), 1057-1066.

Refsgaard, J.C., Madsen, H., Andréassian, V., Arnbjerg-Nielsen, K., Davidson, T. A., Drews, M., Hamilton, D. P., Jeppesen, E., Kjellström, J. E. and Sonnenborg, T. O., 2014. A framework for testing the ability of models to project climate change and its impacts. *Climatic Change*, 122 (1-2), 271-282.

Reich, P. B., Oleksyn, J., Modrzynski, J. and Tjoelker, M. G., 1996. Evidence that longer needle retention of spruce and pine populations at high elevations and high latitudes is largely a phenotypic response. *Tree Physiology,* 16 (7), 643-647.

Reimoser, F., Armstrong, H. and Suchant, R., 1999. Measuring forest damage of ungulates: what should be considered. *Forest Ecology and Management,* 120 (1), 47-58.

Réjou-Méchain, M., Tymen, B., Blanc, L., Fauset, S., Feldpausch, T. R., Monteagudo, A., Phillips, O. L., Richard, H. and Chave, J., 2015. Using repeated small-footprint LiDAR acquisitions to infer spatial and temporal variations of a high-biomass Neotropical forest. *Remote Sensing of Environment, 169*, 93-101.

Rentch, J. S., Schuler, T. M., Nowacki, G. J., Beane, N. R. and Ford, W. M., 2010. Canopy gap dynamics of second-growth red spruce-northern hardwood stands in West Virginia. *Forest Ecology and Management,* 260 (10), 1921-1929.

Rial, J. A., Pielke Sr, R. A., Beniston, M., Claussen, M., Canadell, J., Cox, P., Held, H., de Noblet-Ducoudré, N., Prinn, R. and Reynolds, J. F., 2004. Nonlinearities, feedbacks and critical thresholds within the Earth's climate system. *Climatic Change,* 65 (1-2), 11-38.

Rindfuss, R. R., Walsh, S. J., Turner, B. L., Fox, J. and Mishra, V., 2004. Developing a science of land change: challenges and methodological issues. *Proceedings of the National Academy of Sciences of the United States of America,* 101 (39), 13976-13981.

Rocchini, D., Balkenhol, N., Carter, G. A., Foody, G. M., Gillespie, T. W., He, K. S., Kark, S., Levin, N., Lucas, K., Luoto, M., Nagendra, H., Oldeland, J., Ricotta, C., Southworth, J. and Neteler, M., 2010. Remotely sensed spectral heterogeneity as a proxy of species diversity: recent advances and open challenges. *Ecological Informatics,* 5 (5), 318-329.

Rocha-Santos, L., Pessoa, M. S., Cassano, C. R., Talora, D. C., Orihuela, R. L. L., Mariano-Neto, E., Morante-Filho, J. C., Faria, D. and Cazetta, E., 2016. The shrinkage of a forest: landscape-scale deforestation leading to overall changes in local forest structure. *Biological Conservation,* 196, 1-9.

Rockström, J., Steffen, W., Noone, K., Persson, Å., Chapin, F. S., Lambin, E. F., Lenton, T. M., Scheffer, M., Folke, C., Schellnhuber, H. J., Nykvist, B., de Wit, C. A., Hughes, T., van der Leeuw, S., Rodhe, H., Sörlin, S., Snyder, P. K., Costanza, R., Svedin, U., Falkenmark, M., Karlberg, L., Corell, R. W., Fabry, V. J., Hansen, J., Walker, B., Liverman, D., Richardson, K., Crutzen, P. and Foley, J. A., 2009. A safe operating space for humanity. *Nature,* 461 (7263), 472-475.

Rompré, G., Boucher, Y., Bélanger, L., Côté, S. and Robinson, W. D., 2010. Conserving biodiversity in managed forest landscapes: the use of critical thresholds for habitat. *The Forestry Chronicle,* 86 (5), 589-596.

Rondeux, J. and Sanchez, C., 2010. Review of indicators and field methods for monitoring biodiversity within national forest inventories. Core variable: dead wood. *Environmental Monitoring and Assessment,* 164 (1), 617-630.

Rosa, I. M. D., Ahmed, S. E. and Ewers, R. M., 2014. The transparency, reliability and utility of tropical rainforest land-use and land-cover change models. *Global Change Biology,* 20 (6), 1707-1722.

Royo, A. A., Collins, R., Adams, M. B., Kirschbaum, C. and Carson, W. P., 2010. Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. *Ecology,* 91 (1), 93-105.

Rudel, T. K., Coomes, O. T., Moran, E., Achard, F., Angelsen, A., Xu, J. and Lambin, E., 2005. Forest transitions: towards a global understanding of land use change. *Global Environmental Change,* 15 (1), 23-31.

Rudnick, D., Beier, P., Cushman, S., Dieffenbach, F., Epps, C.W., Gerber, L., Hartter, J., Jenness, J., Kintsch, J., Merenlender, A.M., Perkle, R.M., Preziosi, D.V., Ryan, S.J., and Trombulak., S. C., 2012. *The role of landscape connectivity in planning and implementing conservation and restoration priorities.* Washington, D. C., USA: Ecological Society of America.

Rugani, T., Diaci, J. and Hladnik, D., 2013. Gap dynamics and structure of two old-growth beech forest remnants in Slovenia. *PLoS ONE,* 8 (1), e52641.

Ryan, C. M., Pritchard, R., McNicol, I., Owen, M., Fisher, J. A. and Lehmann, C., 2016. Ecosystem services from southern African woodlands and their future under global change. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 371 (1703).

Ryan, G. M. and Law, E. B., 2005. Interpreting, measuring, and modeling soil respiration. *Biogeochemistry,* 73 (1), 3-27.
Rydgren, K., Økland, R. H. and Hestmark, G., 2004. Disturbance severity and community resilience in a boreal forest. *Ecology*, *85* (7), 1906-1915.
Saab, V. A., Latif, Q. S., Rowland, M. M., Johnson, T. N., Chalfoun, A. D., Buskirk, S. W., Heyward, J. E. and Dresser, M. A., 2014. Ecological consequences of mountain pine beetle outbreaks for wildlife in western North American forests. *Forest Science,* 60 (3), 539-559.
Sabatini, F. M., Burrascano, S., Tuomisto, H. and Blasi, C., 2014. Ground layer plant species turnover and beta diversity in southern-European old-growth forests. *PLoS ONE,* 9 (4), e95244.
Sack, L., 2004. Responses of temperate woody seedlings to shade and drought: do trade-offs limit potential niche differentiation? *Oikos,* 107 (1), 110-127.
Sala, O. E. and Maestre, F. T., 2014. Grass–woodland transitions: determinants and consequences for ecosystem functioning and provisioning of services. *Journal of Ecology,* 102 (6), 1357-1362.
Sanderson, N. A., 2010. Lichens. *In:* Newton, A. C., ed. *Biodiversity in the New Forest*. Newbury, Berkshire, UK: Pisces Publications, 84-112.
Santini, A., Ghelardini, L., de Pace, C., Desprez-Loustau, M. L., Capretti, P., Chandelier, A., Cech, T., Chira, D., Diamandis, S., Gaitniekis, T., Hantula, J., Holdenrieder, O., Jankovsky, L., Jung, T., Jurc, D., Kirisits, T., Kunca, A., Lygis, V., Malecka, M., Marcais, B., Schmitz, S., Schumacher, J., Solheim, H., Solla, A., Szabò, I., Tsopelas, P., Vannini, A., Vettraino, A. M., Webber, J., Woodward, S. and Stenlid, J., 2013. Biogeographical patterns and determinants of invasion by forest pathogens in Europe. *New Phytologist,* 197 (1), 238-250.
Saravesi, K., Markkola, A., Rautio, P., Roitto, M. and Tuomi, J., 2008. Defoliation causes parallel temporal responses in a host tree and its fungal symbionts. *Oecologia,* 156 (1), 117.
Sasaki, T. and Lauenroth, W. K., 2011. Dominant species, rather than diversity, regulates temporal stability of plant communities. *Oecologia*, 166 (3), 761-768.
Sasaki, T., Furukawa, T., Iwasaki, Y., Seto, M. and Mori, A. S., 2015. Perspectives for ecosystem management based on ecosystem resilience and ecological thresholds against multiple and stochastic disturbances. *Ecological Indicators,* 57 (0), 395-408.
Saterson, K. A., Christensen, N. L., Jackson, R. B., Kramer, R. A., Pimm, S. L., Smith, M. D. and Wiener, J. B., 2004. Disconnects in evaluating the relative effectiveness of conservation strategies. *Conservation Biology,* 18 (3), 597-599.
Scheffer, M., 2009. *Critical transitions in nature and society.* Princeton, USA: Princeton University Press.
Scheffer, M., Carpenter, S., Foley, J. A., Folke, C. and Walker, B., 2001. Catastrophic shifts in ecosystems. *Nature,* 413 (6856), 591-596.
Scheffer, M. and Carpenter, S. R., 2003. Catastrophic regime shifts in ecosystems: Linking theory to observation. *Trends in ecology and evolution,* 18 (12), 648-656.
Scheffer, M., Carpenter, S. R., Dakos, V. and Nes, E. H. V., 2015. Generic indicators of ecological resilience: inferring the chance of a critical transition. *Annual Review of Ecology, Evolution, and Systematics,* 46 (1), 145-167.
Scheffer, M., Carpenter, S. R., Lenton, T. M., Bascompte, J., Brock, W., Dakos, V., van de Koppel, J., van de Leemput, I. A., Levin, S. A., van Nes, E. H., Pascual, M. and Vandermeer, J., 2012. Anticipating critical transitions. *Science,* 338 (6105), 344-348.

Scheller, R. M. and Mladenoff, D. J., 2004. A forest growth and biomass module for a landscape simulation model, LANDIS: design, validation, and application. *Ecological Modelling,* 180 (1), 211-229.
Scheller, R. M. and Mladenoff, D. J., 2008. Simulated effects of climate change, fragmentation, and inter-specific competition on tree species migration in northern Wisconsin, USA. *Climate Research,* 36 (3), 191-202.
Scheller, R. M., Domingo, J. B., Sturtevant, B. R., Williams, J. S., Rudy, A., Gustafson, E. J. and Mladenoff, D. J., 2007. Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. *Ecological Modelling,* 201 (3–4), 409-419.
Scheller, R. M., Hua, D., Bolstad, P. V., Birdsey, R. A. and Mladenoff, D. J., 2011. The effects of forest harvest intensity in combination with wind disturbance on carbon dynamics in Lake States Mesic Forests. *Ecological Modelling,* 222 (1), 144-153.
Scheller, R. M., Kretchun, A. M., van Tuyl, S., Clark, K. L., Lucash, M. S. and Hom, J., 2012. Divergent carbon dynamics under climate change in forests with diverse soils, tree species, and land use histories. *Ecosphere,* 3 (11), 1-16.
Scheller, R. M., van Tuyl, S., Clark, K. L., Hom, J. and La Puma, I., 2011. Carbon sequestration in the new jersey pine barrens under different scenarios of fire management. *Ecosystems,* 14 (6), 987.
Schippers, P., van Teeffelen, A. J., Verboom, J., Vos, C. C., Kramer, K. and WallisDeVries, M. F., 2014. The impact of large herbivores on woodland–grassland dynamics in fragmented landscapes: the role of spatial configuration and disturbance. *Ecological Complexity*, 17 (1), 20-31.
Schröder, A., Persson, L. and De Roos, A. M., 2005. Direct experimental evidence for alternative stable states: a review. *Oikos*, 110 (1), 3-19.
Schuler, L. J., Bugmann, H. and Snell, R. S., 2016. From monocultures to mixed-species forests: is tree diversity key for providing ecosystem services at the landscape scale? *Landscape Ecology*, 1-18.
Scottish Executive. 2004. *Scotland's biodiversity: it's in your hands. A strategy for the conservation and enhancement of biodiversity in Scotland.* Edinburgh, UK: Scottish Executive.
Seidensticker, J., 2016. Biodiversity resilience in the Central Indian Highlands is contingent on maintaining and recovering landscape connectivity: the tiger as a case study. *Regional Environmental Change,* 16 (1), 167-179.
Seidl, R., Rammer, W. and Spies, T. A., 2014a. Disturbance legacies increase the resilience of forest ecosystem structure, composition, and functioning. *Ecological Applications*, 24 (8), 2063-2077.
Seidl, R., Schelhaas, M. J., Rammer, W. and Verkerk, P. J., 2014b. Increasing forest disturbances in Europe and their impact on carbon storage. *Nature Climate Change*, 4 (9), 806-810.
Seidl, R., Spies, T. A., Peterson, D. L., Stephens, S. L. and Hicke, J. A., 2016. Review: searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. *Journal of Applied Ecology,* 53 (1), 120-129.
Sett, R. and Kundu, M., 2016. Epiphytic lichens: their usefulness as bio-indicators of air pollution. *Donnish Journal of Environmental Research*, 3, 17-14.
Shade, A., Peter, H., Allison, S., Baho, D., Berga, M., Buergmann, H., Huber, D., Langenheder, S., Lennon, J., Martiny, J., Matulich, K., Schmidt, T. and Handelsman, J., 2012. Fundamentals of microbial community resistance and resilience. *Frontiers in Microbiology,* 3 (417).

Sharma, L. N., Grytnes, J.-A., Måren, I. E. and Vetaas, O. R., 2016. Do composition and richness of woody plants vary between gaps and closed canopy patches in subtropical forests? *Journal of Vegetation Science,* 27 (6), 1129-1139.

Sillett, S. C., McCune, B., Peck, J. E., Rambo, T. R. and Ruchty, A., 2000. Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. *Ecological Applications,* 10 (3), 789-799.

Simard, S. W., Beiler, K. J., Bingham, M. A., Deslippe, J. R., Philip, L. J. and Teste, F. P., 2012. Mycorrhizal networks: mechanisms, ecology and modelling. *Fungal Biology Reviews,* 26 (1), 39-60.

Simons-Legaard, E., Legaard, K., and Weiskittel, A., 2015. Predicting aboveground biomass with LANDIS-II: a global and temporal analysis of parameter sensitivity. *Ecological Modelling,* 313, 325-332.

Simonson, W. D., Allen, H. D. and Coomes, D. A., 2012. Use of an airborne lidar system to model plant species composition and diversity of Mediterranean oak forests. *Conservation Biology,* 26 (5), 840-850.

Simonson, W. D., Allen, H. D. and Coomes, D. A., 2014. Applications of airborne lidar for the assessment of animal species diversity. *Methods in Ecology and Evolution,* 5 (8), 719-729.

Sjöström, E., 1993. *Wood chemistry: fundamentals and applications.* California, USA: Academic Press.

Smith, D. L. and Johnson, L., 2004. Vegetation-mediated changes in microclimate reduce soil respiration as woodlands expand into grasslands. *Ecology,* 85 (12), 3348-3361.

Smithson, M. and Verkuilen, J., 2006. A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. *Psychological Methods,* 11 (1), 54.

Spilsbury, R., 2009. *Deforestation crisis.* New York, USA: The Rosen Publishing Group.

Spurgeon, D. J., Keith, A. M., Schmidt, O., Lammertsma, D. R. and Faber, J. H., 2013. Land-use and land-management change: relationships with earthworm and fungi communities and soil structural properties. *BMC Ecology,* 13 (1), 46.

Staddon, P., Lindo, Z., Crittenden, P. D., Gilbert, F. and Gonzalez, A., 2010. Connectivity, non-random extinction and ecosystem function in experimental metacommunities. *Ecology Letters,* 13 (5), 543-552.

Standish, R. J., Cramer, V. A., Wild, S. L. and Hobbs, R. J., 2007. Seed dispersal and recruitment limitation are barriers to native recolonization of old-fields in western Australia. *Journal of Applied Ecology,* 44 (2), 435-445.

Standish, R. J., Hobbs, R. J., Mayfield, M. M., Bestelmeyer, B. T., Suding, K. N., Battaglia, L. L., Eviner, V., Hawkes, C. V., Temperton, V. M., Cramer, V. A., Harris, J. A., Funk, J. L. and Thomas, P. A., 2014. Resilience in ecology: abstraction, distraction, or where the action is? *Biological Conservation,* 177, 43-51.

Staver, A. C., Archibald, S. and Levin, S. A., 2011. The global extent and determinants of savanna and forest as alternative biome states. *Science,* 334 (6053), 230-232.

Steenberg, J. W. N., Duinker, P. N. and Bush, P. G., 2011. Exploring adaptation to climate change in the forests of central Nova Scotia, Canada. *Forest Ecology and Management,* 262 (12), 2316-2327.

Steffen, W., Richardson, K., Rockström, J., Cornell, S. E., Fetzer, I., Bennett, E. M., Biggs, R., Carpenter, S. R., de Vries, W., de Wit, C. A., Folke, C., Gerten, D., Heinke, J., Mace, G. M., Persson, L. M., Ramanathan, V., Reyers, B. and Sörlin, S., 2015. Planetary boundaries: guiding human development on a changing planet. *Science,* 347 (6223).

Stern, R., 2010. Bryophytes. *In:* Newton, A. C., ed. *Biodiversity in the New Forest*. Newbury, Berkshire, UK: Pisces Publications, 123-124.
Stewart, K. E. J., Bourn, N. a. D. and Thomas, J. A., 2001. An evaluation of three quick methods commonly used to assess sward height in ecology. *Journal of Applied Ecology,* 38 (5), 1148-1154.
Stork, N. E., Boyle, T. J. B., Dale, V., Eeley, H., Finegan, B., Lawes, M., Manokaran, N., Prabhu, R. and Soberon, J., 1997. *Criteria and indicators for assessing the sustainability of forest management: conservation of biodiversity*. Jakarta, Indonesia: CIFOR. CIFOR Working Paper 17.
Stuart, G. W., and Edwards, P. J., 2006. Concepts about forests and water. *Northern Journal of Applied Forestry,* 23 (1), 11-19.
Štursová, M., Snajdr, J., Cajthaml, T., Barta, J., Santruckova, H. and Baldrian, P., 2014. When the forest dies: the response of forest soil fungi to a bark beetle-induced tree dieback. *ISME J,* 8 (9), 1920-1931.
Suding, K. N. and Hobbs, R. J., 2009. Threshold models in restoration and conservation: a developing framework. *Trends in Ecology and Evolution,* 24 (5), 271-279.
Summerville, K. S. and Crist, T. O., 2001. Effects of experimental habitat fragmentation on patch use by butterflies and skippers (Lepidoptera). *Ecology,* 82 (5), 1360-1370.
Sumnall, M. J., 2013. *The assessment of habitat condition and conservation status of lowland British woodlands using earth observation techniques.* Thesis (PhD). Bournemouth University.
Sumnall, M. J., Hill, R. A. and Hinsley, S. A., 2016. Comparison of small-footprint discrete return and full waveform airborne lidar data for estimating multiple forest variables. *Remote Sensing of Environment,* 173, 214-223.
Sutherland, W. J., 2000. *The conservation handbook: research, management and policy.* Oxford, UK: Blackwell Science.
Sutherland, W. J., Mitchell, R., Walsh, J., Amano, T., Ausden, M., Beebee, T. J. C., Bullock, D., Daniels, M., Deutsch, J., Griffiths, R. A., Prior, S. V., Whitten, T. and Dicks, L. V., 2013. Conservation practice could benefit from routine testing and publication of management outcomes. *Conservation Evidence,* 10, 1-3.
Swatantran, A., Dubayah, R., Roberts, D., Hofton, M. and Blair, J. B., 2011. Mapping biomass and stress in the Sierra Nevada using lidar and hyperspectral data fusion. *Remote Sensing of Environment,* 115 (11), 2917-2930.
Sweeney, O.F.M., Wilson, M.W., Irwin, S., Kelly, T.C. and O'Halloran, J., 2010. Are bird density, species richness and community structure similar between native woodlands and non-native plantations in an area with a generalist bird fauna? *Biodiversity and Conservation,* 19 (8), 2329-2342.
Syrbe, R.U. and Walz, U., 2012. Spatial indicators for the assessment of ecosystem services: providing, benefiting and connecting areas and landscape metrics. *Ecological Indicators*, 21, 80-88.
Tambosi, L. R., Martensen, A. C., Ribeiro, M. C. and Metzger, J. P., 2014. A framework to optimize biodiversity restoration efforts based on habitat amount and landscape connectivity. *Restoration Ecology,* 22 (2), 169-177.
Tanner, E.V.J. and Bellingham, P.J., 2006. Less diverse forest is more resistant to hurricane disturbance: evidence from montane rain forests in Jamaica. *Journal of Ecology*, 94 (5), 1003-1010.
Tapia-Armijos, M. F., Homeier, J., Espinosa, C. I., Leuschner, C. and de la Cruz, M., 2015. Deforestation and forest fragmentation in south Ecuador since the 1970s – losing a hotspot of biodiversity. *PLoS ONE,* 10 (9), e0133701.

Tarvainen, O., Hekkala, A. M., Kubin, E., Tamminen, P., Murto, T. and Tolvanen, A., 2015. Soil disturbance and early vegetation response to varying intensity of energy wood harvest. *Forest Ecology and Management*, 348, 153-163.

Taylor, P. D., Fahrig, L., Henein, K. and Merriam, G., 1993. Connectivity is a vital element of landscape structure. *Oikos*, 68 (3), 571-573.

Temperli, C., Bugmann, H. and Elkin, C., 2012. Adaptive management for competing forest goods and services under climate change. *Ecological Applications*, 22 (8), 2065-2077.

Teste, F. P. and Simard, S. W., 2008. Mycorrhizal networks and distance from mature trees alter patterns of competition and facilitation in dry Douglas-fir forests. *Oecologia*, 158 (2), 193-203.

The African Development Bank, 2013. *At the center of Africa's transformation: strategy for 2013–2022* [online]. African Development Bank Group. Available from: https://www.afdb.org/fileadmin/uploads/afdb/Documents/Policy-Documents/AfDB_Strategy_for_2013%E2%80%932022_-_At_the_Center_of_Africa%E2%80%99s_Transformation.pdf [Accessed March 2016].

Thom, D. and Seidl, R., 2016. Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. *Biological Reviews*, 91 (3), 760-781.

Thompson, D. A. and Matthews, R. W., 1989. *The storage of carbon in trees and timber*. Forestry Commission. Surrey, UK: Forestry Commission. Research information note 160.

Thompson, I., Mackey, B., McNulty, S. and Mosseler, A., 2009. *Forest resilience, biodiversity, and climate change. A synthesis of the biodiversity/resilience/stability relationship in forest ecosystems.* Technical Series no. 4.3. Montreal, Canada: Secretariat of the Convention on Biological Diversity.

Tinkham, W. T., Smith, A. M. S., Hoffman, C., Hudak, A. T., Falkowski, M. J., Swanson, M. E. and Gessler, P. E., 2012. Investigating the influence of lidar ground surface errors on the utility of derived forest inventories. *Canadian Journal of Forest Research*, 42 (3), 413-422.

Tinya, F., Márialigeti, S., Király, I., Németh, B. and Ódor, P., 2009. The effect of light conditions on herbs, bryophytes and seedlings of temperate mixed forests in Őrség, western Hungary. *Plant Ecology*, 204 (1), 69-81.

Treu, R., Karst, J., Randall, M., Pec, G. J., Cigan, P. W., Simard, S. W., Cooke, J. E. K., Erbilgin, N. and Cahill, J. F., 2014. Decline of ectomycorrhizal fungi following a mountain pine beetle epidemic. *Ecology*, 95 (4), 1096-1103.

Trumbore, S., Brando, P. and Hartmann, H., 2015. Forest health and global change. *Science*, 349 (6250), 814-818.

Tubbs, C. R., 2001. *The New Forest: history, ecology and conservation.* Hampshire, UK: New Forest Ninth Centenary Trust.

Turner, M. G., 2010. Disturbance and landscape dynamics in a changing world. *Ecology*, 91 (10), 2833-2849.

Turner, M. G., Donato, D. C. and Romme, W. H., 2013. Consequences of spatial heterogeneity for ecosystem services in changing forest landscapes: priorities for future research. *Landscape Ecology*, 28 (6), 1081-1097.

Turner, W., Spector, S., Gardiner, N., Fladeland, M., Sterling, E. and Steininger, M., 2003. Remote sensing for biodiversity science and conservation. *Trends in Ecology and Evolution*, 18 (6), 306-314.

Turnhout, E., Hisschemöller, M. and Eijsackers, H., 2007. Ecological indicators: between the two fires of science and policy. *Ecological Indicators,* 7 (2), 215-228.
Uhl, C., Clark, K., Dezzeo, N. and Maquirino, P., 1988. Vegetation dynamics in Amazonian treefall gaps. *Ecology,* 69 (3), 751-763.
USDA, 2012. *Major forest insect and disease conditions in the United States: 2011* [online]. Washington, D. C., USA: United States Department of Agriculture Forest Service. Available from: https://www.fs.fed.us/foresthealth/publications/ConditionsReport_2011.pdf [Accessed November 2015].
van Couwenberghe, R., Collet, C., Lacombe, E. and Gégout, J.-C., 2011. Abundance response of western European forest species along canopy openness and soil pH gradients. *Forest Ecology and Management,* 262 (8), 1483-1490.
van der Werf, G. R., Morton, D. C., DeFries, R. S., Olivier, J. G. J., Kasibhatla, P. S., Jackson, R. B., Collatz, G. J. and Randerson, J. T., 2009. CO_2 emissions from forest loss. *Nature Geoscience,* 2 (11), 737-738.
van Ewijk, K. Y., Randin, C. F., Treitz, P. M. and Scott, N. A., 2014. Predicting fine-scale tree species abundance patterns using biotic variables derived from lidar and high spatial resolution imagery. *Remote Sensing of Environment,* 150, 120-131.
van Mantgem, P. J. and Stephenson, N. L., 2007. Apparent climatically induced increase of tree mortality rates in a temperate forest. *Ecology Letters,* 10 (10), 909-916.
van Mantgem, P. J., Stephenson, N. L., Byrne, J. C., Daniels, L. D., Franklin, J. F., Fulé, P. Z., Harmon, M. E., Larson, A. J., Smith, J. M., Taylor, A. H. and Veblen, T. T., 2009. Widespread increase of tree mortality rates in the western United States. *Science,* 323 (5913), 521-524.
van Nes, E. H. and Scheffer, M., 2005. Implications of spatial heterogeneity for catastrophic regime shifts in ecosystems. *Ecology,* 86 (7), 1797-1807.
van Nes, E. H. and Scheffer, M., 2007. Slow recovery from perturbations as a generic indicator of a nearby catastrophic shift. *The American Naturalist,* 169 (6), 738-747.
Vanderwel, M. C., Coomes, D. A. and Purves, D. W., 2013. Quantifying variation in forest disturbance, and its effects on aboveground biomass dynamics, across the eastern United States. *Global Change Biology,* 19 (5), 1504-1517.
Vázquez, D. P., 2002. Multiple effects of introduced mammalian herbivores in a temperate forest. *Biological Invasions,* 4 (1), 175-191.
Ver Hoef, J. M. and Boveng, P. L., 2007. Quasi-Poisson vs. negative binomial regression: how should we model overdispersed count data? *Ecology,* 88 (11), 2766-2772.
Vera, F. W. M., 2000. *Grazing ecology and forest history.* Wallingford, UK: CABI publishing.
Vergés, A., Vanderklift, M. A., Doropoulos, C. and Hyndes, G. A., 2011. Spatial patterns in herbivory on a coral reef are influenced by structural complexity but not by algal traits. *PLoS ONE,* 6 (2), e17115.
Vickerman, S. and Kagan, J. S., 2014. *Assessing ecological integrity across jurisdictions and scales* [online]. Oregon Biodiversity Information Center, Institute for Natural Resources. Available from: http://ir.library.oregonstate.edu/xmlui/bitstream/handle/1957/54180/Assessing%20Ecological%20Integrity_final%20report.pdf?sequence=3 [Accessed December 2016].

Vierling, K. T., Swift, C. E., Hudak, A. T., Vogeler, J. C. and Vierling, L. A., 2014. How much does the time lag between wildlife field-data collection and lidar-data acquisition matter for studies of animal distributions? A case study using bird communities. *Remote Sensing Letters*, 5 (2), 185-193.

Vitousek, P. M., Cassman, K., Cleveland, C., Crews, T., Field, C. B., Grimm, N. B., Howarth, R. W., Marino, R., Martinelli, L., Rastetter, E. B. and Sprent, J. I., 2002. Towards an ecological understanding of biological nitrogen fixation. *Biogeochemistry*, 57 (1), 1-45.

Walker, B., Carpenter, S., Rockstrom, J., Crépin, A. S. and Peterson, G., 2012. Drivers," slow" variables," fast" variables, shocks, and resilience. *Ecology and Society*, 17 (3).

Walker, B., Holling, C. S., Carpenter, S. R. and Kinzig, A., 2004. Resilience, adaptability and transformability in social-ecological systems. *Ecology and society*, 9 (2).

Walker, B. H. and Salt, D., 2012. *Resilience practice: building capacity to absorb disturbance and maintain function.* Washington D. C., USA: Island Press.

Walters, C. J., 1986. *Adaptive management of natural resources.* New York, USA: McGraw-Hill.

Wang, C.-H. and Blackmore, J. M., 2009. Resilience concepts for water resource systems. *Journal of Water Resources Planning and Management*, 135 (6), 528-536.

Wang, S. and Loreau, M., 2014. Ecosystem stability in space: α, β and γ variability. *Ecology Letters*, 17 (8), 891-901.

Wang, Y., Gril, J., Clair, B., Minato, K. and Sugiyama, J., 2010. Wood properties and chemical composition of the eccentric growth branch of *Viburnum odoratissimum* var. *awabuki*. Trees, 24 (3), 541-549.

Wardle, D. A., Bardgett, R. D., Klironomos, J. N., Setälä, H., van der Putten, W. H. and Wall, D. H., 2004. Ecological linkages between aboveground and belowground biota. *Science*, 304 (5677), 1629-1633.

Washington, H., Baillie, J., Waterman, C. and Milner-Gulland, E., 2014. A framework for evaluating the effectiveness of conservation attention at the species level. *Oryx*, 49 (03), 481-491.

Washington-Allen, R., Ramsey, R., West, N. and Norton, B., 2008. Quantification of the ecological resilience of drylands using digital remote sensing. *Ecology and Society*, 13 (1).

Watson, J. E. M., Dudley, N., Segan, D. B. and Hockings, M., 2014. The performance and potential of protected areas. *Nature*, 515 (7525), 67-73.

Watts, K., Griffiths, M., Quine, C., Ray, D. and Humphrey, J., 2005. *Towards a woodland habitat network for Wales.* Bangor, UK: Countryside Council for Wales. Contract science report 686.

Wearn, O. R., Reuman, D. C. and Ewers, R. M., 2012. Extinction debt and windows of conservation opportunity in the Brazilian Amazon. *Science*, 337 (6091), 228-232.

Westgate, M. J., Likens, G. E. and Lindenmayer, D. B., 2013. Adaptive management of biological systems: a review. *Biological Conservation*, 158, 128-139.

Wickham, H., 2009. *ggplot2: elegant graphics for data analysis.* New York, USA: Springer Verlag.

Wikramanayake, E., Dinerstein, E., Seidensticker, J., Lumpkin, S., Pandav, B., Shrestha, M., Mishra, H., Ballou, J., Johnsingh, A. J. T., Chestin, I. and Sunarto, S., 2011. A landscape-based conservation strategy to double the wild tiger population. *Conservation Letters*, 4 (3), 219-227.

Williams, J., 2006. Monitoring the condition of UK protected sites: results from the first six years. *British Wildlife*, 18, 1-9.
Witman, J.D. and Roy, K., 2009. *Marine macroecology*. Chicago, Illinois, USA: University of Chicago Press.
Wolf, J., Fricker, G., Meyer, V., Hubbell, S., Gillespie, T. and Saatchi, S., 2012. Plant species richness is associated with canopy height and topography in a neotropical forest. *Remote Sensing,* 4 (12), 4010.
Woodall, C. W., Oswalt, C. M., Westfall, J. A., Perry, C. H., Nelson, M. D. and Finley, A. O., 2009. An indicator of tree migration in forests of the eastern United States. *Forest Ecology and Management,* 257 (5), 1434-1444.
Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., Jackson, J. B. C., Lotze, H. K., Micheli, F., Palumbi, S. R., Sala, E., Selkoe, K. A., Stachowicz, J. J. and Watson, R., 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science,* 314 (5800), 787-790.
Wright, R. N. and Westerhoff, D. V., 2001. *New Forest SAC management plan.* Lyndhurst, Hampshire, UK: English Nature.
Yu, D. W., Ji, Y., Emerson, B. C., Wang, X., Ye, C., Yang, C. and Ding, Z., 2012. Biodiversity soup: metabarcoding of arthropods for rapid biodiversity assessment and biomonitoring. *Methods in Ecology and Evolution*, 3 (4), 613-623.
Zavaleta E.S. and Chapin III, F. S., 2010. Resilience frameworks: enhancing the capacity to adapt to change. *In*: Cole, D. N. and Yung, L., eds. *Beyond naturalness: rethinking park and wilderness stewardship in an era of rapid change*. Washington D. C., USA: Island Press. 142-161.
Zeileis, A., Cribari-Neto, F., Gruen, B., Kosmidis, I., Simas, A. B. and Rocha, A. V., 2016. Package 'betareg' [online]. Available from: https://cran.r-project.org/web/packages/betareg/betareg.pdf [Accessed September 2015].
Zeileis, A. and Hothorn, T., 2002. Diagnostic checking in regression relationships. *R News,* 2 (3), 7-10.
Zellweger, F., Morsdorf, F., Purves, R. S., Braunisch, V. and Bollmann, K., 2014. Improved methods for measuring forest landscape structure: lidar complements field-based habitat assessment. *Biodiversity and Conservation,* 23 (2), 289-307.
Zenner, E. K., Kabrick, J. M., Jensen, R. G., Peck, J. E. and Grabner, J. K., 2006. Responses of ground flora to a gradient of harvest intensity in the Missouri Ozarks. *Forest Ecology and Management,* 222 (1–3), 326-334.
Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A. and Smith, G. M., 2009. *Mixed effects models and extensions in ecology with R.* New York, USA: Springer New York.

Appendix 2.1: Additional experimental design details for Chapter 2

Measurement of DBH

The diameters at breast height (DBH) of both living and dead standing trees (snags) were measured at 1.3 m using a diameter tape pulled taut horizontally to the trunk. Following advice and procedures from Husch et al. (2003) and van Laar and Akça (2007), specific instructions were followed when using diameter tapes for difficult trees. The combined DBHs were used to calculate the overall BA (Cantarello and Newton, 2008), forming the basis of the primary criterion.

Crown condition

Living beech trees were assessed for their condition, which was undertaken using binoculars at several points around each tree where visibility was good. The condition attributes were the potential crown loss, live growth loss, condition of the current branches and discolouration of the crown. Potential crown loss and leaf loss were recorded as a percentage based on the average values provided by two observers. Overall condition was recorded as number (1-5), with 1 denoting a healthy tree and 5 denoting a dead tree. Any pathogens present were also recorded after a thorough search of the lower sections of each tree.

Canopy openness

At each corner of the 10 x 10 m sub-plot four readings were taken using a spherical densiometer, one in each cardinal direction, giving an overall average for that plot (Strickler, 1959).

Understorey openness

Understorey openness was determined the same way as canopy openness, but only for trees less than approximately 6 m in height.

Forest biomass

Following Jenkins et al. (2011), oven-dry biomass was determined in four different components of the stand; the roots, the tree stems, the branches and foliage. Specifically, the quadratic mean DBH of all the trees in a plot were calculated based on their BA. This number was then used to calculate the mean total tree volume which was then multiplied

by a species-specific Nominal Specific Gravity value, found in Jenkins et al. (2011), to estimate the total oven-dry biomass of each stem. To calculate the total biomass of a single species, the stem biomass, crown biomass and root biomass were summed together and multiplied by the number of that species present in the plot. The total biomass of all species was then calculated by summating all individual species' biomass values. The oven-dry biomass was calculated based on specific values for broadleaves, taken form McKay et al. (2003).

Carbon assessment for trees

Carbon content of a plot was calculated by multiplying the oven-dry matter biomass by 0.5, the carbon fraction of biomass (Matthews, 1993).

Herbivore pressure metrics

To account for the relative presence and influence of herbivores, understorey crown condition, browseline, sward height, seedling and sapling abundance, browsing intensity, dung counts, and presence of a shrub layer were recorded.

For living trees in the understorey, crown condition (average of two different observers) was recorded based on deviation from perceived 'pristine' condition (i.e. 100%). Percentage of discolouration, percentage of leaves remaining, potential crown structure, empty branches and position of the tree were all considered.

The browse lines of palatable (e.g. beech, oak, birch) and unpalatable (e.g. holly, hawthorn) trees were recorded if they were within the edges of the plot. Using a marked range pole, any branches that were higher than 1.8 m (a deer's maximum browse height), but lower than 2.3 m (based on an average drop of 50 cm in the winter), were counted as browsed. Any branches that retained leaves below 1.8 m were counted as unbrowsed. A percentage ratio of browsed to unbrowsed was calculated. The sward height was measured using a measuring stick, based on the findings of Stewart et al. (2001). This was measured in the centre and at the four corners of the sub-plot, and a mean value was recorded.

The percentages cover of mosses, bare ground, bracken, trampling and ground flora were recorded from a detailed visual assessment of each plot. Similarly, seedling (< 1.3 m in height) and sapling (> 1.3 m and DBH < 10 cm) abundances were assessed through a manual search of the entire 20 x 20 m plot. Seedlings were any counted if they were older than a year, based on physical aspects.

Partial defoliation or complete consumption of plants occur through herbivore browsing, the intensity of which is commonly determined by counts of un-browsed and browsed branches (Bergström and Guillet, 2002; Gibson, 2002). This was undertaken using a stratified random sampling design. Initially, a 2 x 2 m quadrat was placed in the most south-westerly corner of the sub-plot, continuing clockwise (NW, NE, SE) around the corners, until 100 stems had been assessed. The same technique was used for assessing bramble browsing, following Bazely et al. (1991).

For estimating herbivore abundance from dung, the faecal standing crop (FSC) method, the most commonly used and efficient technique (Marques et al. 2001; Campbell et al. 2004), was used. A manual dung count was carried out in the sub-plot; the amount, condition and the species recorded. Following Jenkins and Manly (2008), the individual pellets/ bolus and their condition were recorded. The faecal matter of different animals (deer, *Equus* species, rabbits and cattle) were recorded separately.

Soil survey

Following the methods of DeLuca et al. (2013), ten separate soil samples were taken, two from the centre and two at each corner of the nested 10 x 10 m sub-plot, for both the O horizon and A horizon soil layer (0-15 cm below the O horizon). The vegetation the sample was taken under (e.g. bracken, grass) was noted.

For bulk density (BD) measurements, three 100 cm^3 stainless steel rings were inserted into the soil to ensure a known volume. These were taken from the SW and NE corners and from the mid-point.

For analyses of NO_3^- and NH_4^+, 5 g of sieved, field-moist soil was placed into a labelled tube with 25 ml of 1 M KCl added. The soils were shaken by hand and placed horizontally on a rotary shaker for 30 minutes at 250 rev/min. The extracts were immediately filtered through a Fisher QT 210 filter paper into a labelled polypropylene vial. The filtrates were then frozen immediately and analysed two months later. Both NH_4^+ and NO_3^- were analysed using the microplate-colorimetric technique, with the salicylate-nitroprusside method for NH_4^+, following Mulvaney (1996) and the vanadium method for NO_3^- (Miranda et al. 2001).

To determine the potential mineralisable nitrogen concentrations, 5 g of sieved, field-moist soil was placed into a labelled tube with 25 ml of ultrapure water added. The headspace was then flushed with N_2 (g). The tube was sealed and incubated for 7 days at 40°C (Keeney, 1982). Immediately after incubation, 1.75 g of KCl was added to each tube. The tubes were shaken (1 hr at 200 rev/min), centrifuged and filtered immediately,

using the process as for NO_3^- and NH_4^+. The pH and electrical conductivity of soil was determined using a 2:1 distilled water to soil ratio.

Net N mineralisation and nitrification

To enable analysis of in-situ nitrification and N mineralisation rates, following DeLuca et al. (2013), a polyester mesh ionic resin capsule (Unibest, Walla Walla, WA, USA) was buried in the centre of each plot, 10 cm deep into the mineral layer. The capsules were placed between 9th October and 12th November 2014 and were removed from the ground four months later.

The nitrogen mineralisation and nitrification of a plot were analysed through leaching of resin capsules (RC). Initially, 10 mL of 1M KCl was placed into each tube containing a RC, which was then shaken horizontally for 30 minutes at 250 rpm. The extractant was poured into a clean storage tube. This process was repeated two more times, making a total of 30 mL of the extractant. The extractant was centrifuged at 4000 rpm for 10 minutes. 20 mL of the supernatant was then pipetted into a 30 mL polypropylene tube and frozen prior to analysis.

Soil respiration rate

Soil respiration rate was measured using a SR-1 closed chamber Infra-red gas analyser (PP Systems, Amesbury, MA, USA). All measurements were recorded between 10:00 and 14:00 on sunny days within a month of each other. After automatic flushing and calibration of the chamber, the PVC chamber was inserted 2 cm into the soil after any vegetation had been removed from the surface. The CO_2 concentration was measured continuously for 2 minutes. Five measurements were taken from each survey plot and then averaged to produce a mean soil respiration rate for the whole plot. Soil respiration rate was calculated as in (PP Systems, 2010):

$$R=V/A \times ((Cn-Co)/(Tn))$$

Where R is the respiration rate, V is the volume of the chamber, A is the area of soil exposed, Cn is the CO_2 concentration at time 0, and Co is the CO_2 concentration at time, Tn (120 seconds in this study).

Soil moisture

Soil moisture was measured as the difference in weight of a 5 g moist soil sample before and after oven-drying. Sieved mineral and organic samples were oven-dried at 105 °C and 80 °C, respectively, until they remained a constant weight. To measure the soil organic matter (SOM), the oven-dried samples were then placed in a 500 °C furnace overnight (12 hours), the final weight recorded after being cooled in a desiccator. LOI = 100 x (mass of oven-dry soil-mass of ignited soil)/ mass of oven-dry soil = g per 100g oven-dry soil (Rowell, 1994). The soil was dried at 105 °C for 24 h and then sieved (2 mm) to remove stones and other non-soil material (>2 mm diameter). Bulk density was calculated by dividing soil mass (less stone mass) by core volume (less stone volume).

Soil content and structure

The Forest Research (FR) team at Alice Holt Lodge, Surrey, measured the exchangeable cations of K, S, Ca, Mg, Na, Al, Mn and F; total N and C, organic and inorganic C; the P available; and the particle sizes of the soil from air-dried samples. Following FR methods, the exchangeable cations were analysed using $BaCl_2$ extraction (FR Reference method: ISO 11260 and 14254). First, a soil suspension of 3 g soil and 36 ml of 0.1 M $BaCl_2$ was shaken for 60 minutes, centrifuged and filtered with 0.45 µm syringe filter. Extracts were then acidified and analysed using a dual view ICP-OES (Thermo ICap 6500 duo). The P Olsen method with ADAS index was used to determine the amount of phosphorus available (FR Reference method: The analysis of Agricultural Materials MAFF 3rd Edition RB427). A suspension of 5 g soil with 100 ml of sodium bicarbonate solution was buffered at pH 8.5. The solution was shaken for 30 min on an orbital shaker, centrifuged and filtered with 0.45µm syringe filters. Extracts were then acidified with 1.5 M sulphuric acid and mixed with a solution of ascorbic acid and ammonium molybdate for 10 min and then measured at 880 nm with a Shimadzu UV sprectrophotometer. Total C and N were analysed using a Carlo Erba CN analyser (Flash1112 series) and combustion method (FR Reference method: ISO 10694 and 13878). Samples were ball-milled for homogenisation and then around 30 mg weighed in tin capsules, pressed and measured using the analyser. Following, 30 g of soil was placed in a silver capsule to quantify inorganic C. The silver capsule was put furnace at 500^{o}C for 2 hours, which removed the organic carbon. The organic carbon fraction was calculated as the difference between total carbon and inorganic carbon. The soil Particle Size Distribution was determined using a Laser Diffraction Particle Sizer (FR Reference method: Laser diffraction); 30 g of soil were suspended in water and passed through the flow cell of the analyser (Beckman Coulter LS13320).

Appendix 2.2: Ground-dwelling arthropod collection and analysis for Chapter 2

Ground-dwelling arthropods collection

Pitfall trapping was carried out in five out of the 12 sites. In each site eight pitfall traps were placed on the perimeter of the 10m x 10m sub-plot; one in each corner and one midway along each edge. A soil auger was used to create holes in which plastic cups (8 cm in diameter and 11 cm tall) were placed. Approximately 3cm of propylene glycol, a cost-effective preservative, was poured into each cup. Water was allowed to escape through the use of drainage holes in the top of the cups; this also prevented the trap flooding. A galvanised steel square which was supported by turned-down corners was placed over each trap. Forestry Commission staff collected the contents of each pitfall trap weekly from late May to late July 2014, totalling eight collections and 56 trapping days. The arthropod material from the eight pitfall traps in each plot were pooled into a single labelled and sterilised 1 litre sample bottle and then stored in -5 °C to preserve the specimens for metabarcoding.

Ground-dwelling arthropods analysis

DNA metabarcoding was employed for invertebrate identification using a methodology tailored from the approach described in Yu et al. (2012). Samples were stored in absolute ethanol at 4°C, followed by the extraction of DNA using the Qiagen blood and tissue extraction kit. Polymerase Chain Reactions (PCR) were performed targeting the 658 base pair C terminal region in the gene encoding the mitochondrial cytochrome oxidase subunit I (COI); primers used for the COI region of interest were: Forward: LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and Reverse: mlCOIintGLR (5'-GGNGGR TANANNGTYCANCCNGYNCC-3'). Three separate PCRs were carried out for each sample. An aliquot was checked on a 1.4% agarose gel and then the PCRs pooled before library construction. A multiplex identifier (MID) tag was attached to the forward primer in addition to the relevant adaptor for the sequencing platform. The MID tag was specific to each sample and allowed multiple samples to be pooled for sequencing and then separated out bioinformatically afterwards. A touch-down thermocycling profile was used, followed by a low number of cycles with an intermediate annealing temperature. Indexing barcodes were added to the amplicons following the Illumina TruSeq Nano protocol from the ‘Clean-up Fragmented DNA’ stage. In a deviation from this protocol fragments were size-selected using blue Pippin size selection of the 300-670bp region to

remove larger fragments. The barcoded samples were pooled into a single pool and 250bp paired end reads were generated on one lane of the Illumina MiSeq platform. The pool was demultiplexed into the individual samples using the Illumina bcl2fastq (v 1.8.4bin) software. The samples were clustered into OTUs (operational taxonomic units) using the approach described in Yu et al. (2012) starting with demultiplexed samples in step 1. Instead of the described step 6 of the pipeline we used the BOLD database and website for taxonomic assignment and confidence assessment. Accepted matches had to have at least 97% sequence similarity at a given taxonomic level. For this we queried the website by using a custom script that created the urls and parsed the output for each OTU. In a final step the taxonomic assignment, OTU and the number of reads of each sample mapping to the OTUs was collated into a single table. The final species lists were checked against previous records of species occurrence in Britain using primarily the National Biodiversity Networks Gateway (NBN Gateway, 2015), but also Fauna Europaea (de Jong et al. 2014), Antweb (AntWeb, 2015), the British Arachnological Society (British Arachnological Society, 2015) and Araneae: Spiders of Europe (Nentwig et al. 2015). Where no previous record was found to species level, occurrence in Britain to Genus level was checked.

Appendix 2.3: Field-collected variables used in Chapter 2.

Table A2.3: Variables and their units recorded for Chapter 2.

Variable	Biodiversity (B), ecosystem function (EF) or ecosystem condition (EC) measure?	Units
Ectomycorrhizal fungi species richness	B	Unique species 0.04 ha^{-1}
Sward height	EC	cm
Abundance of holly seedlings	EC	Individuals 0.04 ha^{-1}
Abundance of beech seedlings	EC	Individuals 0.04 ha^{-1}
Abundance of oak seedlings	EC	Individuals 0.04 ha^{-1}
Abundance of tree seedlings	EC	Individuals 0.04 ha^{-1}
Abundance of palatable seedlings	EC	Individuals 0.04 ha^{-1}
Bulk density of the soil	EC	g cm^{-3}
Depth of the organic layer	EC	cm
Average diameter at breast height of beech trees	EC	cm
Average height of beech trees	EC	M
Volume of standing dead wood in a plot	EC	m^3 ha^{-1}
Volume of lying dead wood in a plot	EC	m^3 ha^{-1}
C/N ratio of the soil	EF	C/N ratio
Potassium exchangeable cations concentration in the mineral layer soil	EF	cmol(+)/kg
Magnesium exchangeable cations concentration in the mineral layer soil	EF	cmol(+)/kg
Sodium exchangeable cations concentration in the mineral layer soil	EF	cmol(+)/kg
Calcium exchangeable cations concentration in the mineral layer soil	EF	cmol(+)/kg
Manganese exchangeable cations concentration in the mineral layer soil	EF	cmol(+)/kg

Iron exchangeable cations concentration in the mineral layer soil	EF	cmol(+)/kg
Aluminium exchangeable cations concentration in the mineral layer soil	EF	cmol(+)/kg
Availability of soil phosphorus	EF	mg kg^{-1}
Total soil nitrogen	EF	% of soil
Total soil carbon	EF	% of soil
Soil pH	EF	pH
Electrical conductivity	EF	mS m^{-1}
Net ammonification	EF	µg NH_4^+ $capsule^{-1}$ mon^{-1}
Net nitrification	EF	µg NO_3^- $capsule^{-1}$ mon^{-1}
Net mineralisation	EF	µg NH_4^+ and NO_3^- $capsule^{-1}$ mon^{-1}
Soil respiration rate	EF	µmol m^{-2} s^{-1}
Soil temperature	EF	°C
Total stand carbon (vegetation, dead wood and soil)	EF	t ha^{-1}
Aboveground biomass	EC	t ha^{-1}
Soil clay percentage	EC	% 0-2 µm soil particles
Soil silt percentage	EC	% 2-63 µm soil particles
Soil sand percentage	EC	% 63 µm-2 mm soil particles
Bracken cover	EC	% cover 0.04 ha^{-1}
Bare ground and moss cover	EC	% cover 0.04 ha^{-1}
Litter cover	EC	% cover 0.04 ha^{-1}
Grass cover	EC	% cover 0.04 ha^{-1}
Palatable tree browseline	EC	% browseline (above 1.8 m) 0.04 ha^{-1}
Unpalatable tree browseline	EC	% browseline (above 1.8 m) 0.04 ha^{-1}
Holly cover	EC	% cover 0.04 ha^{-1}
***Rubus* cover**	EC	% cover 0.04 ha^{-1}
Holly shrubs browsed	EC	% browse of available plants
***Rubus* shrubs browsed**	EC	% browse of available plants
Average crown condition	EC	% condition

Understorey condition	EC	% condition
Canopy openness	EC	% sky visible
Understorey openness	EC	% sky visible
Tree seedling richness	B	Unique species 0.04 ha^{-1}
Tree sapling richness	B	Unique species 0.04 ha^{-1}
Spider species richness	B	Unique species 0.04 ha^{-1}
Rove beetle species richness	B	Unique species 0.04 ha^{-1}
Carabid beetle species richness	B	Unique species 0.04 ha^{-1}
Ant species richness	B	Unique species 0.04 ha^{-1}
Weevil species richness	B	Unique species 0.04 ha^{-1}
Woodlice species richness	B	Unique species 0.04 ha^{-1}
Ground-dwelling arthropod species richness	B	Unique species 0.04 ha^{-1}
Moisture content of the mineral layer	EF	% soil moisture
Moisture content of the organic layer	EF	% soil moisture
***Cervus* dung proportional**	EC	see Jenkins and Manly (2008)
***Equus* dung proportional**	EC	see Jenkins and Manly (2008)
Proportional dung total	EC	see Jenkins and Manly (2008)
Very large beech trees (74.97 cm < dbh < 103 cm)	EC	Individuals 0.04 ha^{-1}
Large beech trees (68.32 cm < dbh < 74.97 cm)	EC	Individuals 0.04 ha^{-1}
Holly tree abundance	EC	Individuals 0.04 ha^{-1}
Beech trees abundance	EC	Individuals 0.04 ha^{-1}
Holly saplings abundance	EC	Individuals 0.04 ha^{-1}
Beech saplings abundance	EC	Individuals 0.04 ha^{-1}
Overall saplings abundance	EC	Individuals 0.04 ha^{-1}
Ground flora species richness	B	Unique species 0.04 ha^{-1}
Woody ground flora species richness	B	Unique species 0.04 ha^{-1}
Non-woody ground flora species richness	B	Unique species 0.04 ha^{-1}
Lichen species richness	B	Unique species 0.04 ha^{-1}
Lichen species richness on holly	B	Unique species 0.04 ha^{-1}
Lichen species richness on beech	B	Unique species 0.04 ha^{-1}
Organic layer loss on ignition	EC	% weight loss
Mineral layer loss on ignition	EC	% weight loss
Organic layer nitrate concentration	EF	mg kg^{-1}

Mineral layer nitrate concentration	EF	mg kg^{-1}
Organic layer ammonium concentration	EF	mg kg^{-1}
Mineral layer ammonium concentration	EF	mg kg^{-1}
Potentially mineralisable nitrogen of the organic layer	EF	μg g^{-1}
Potentially mineralisable nitrogen of the mineral layer	EF	μg g^{-1}
Understorey biomass	EC	t ha^{-1}

Appendix 2.4: GLM results for Chapter 2.

Table A2.4: Generalised linear mixed models used to determine whether a threshold was exhibited in all the response variables and associated measures of parsimony (AICc), support (ΔAICc, AICc weight) and goodness of fit (Marginal r^2). Mod_cont_NL specifies that the model contained a linear and quadratic term of BA loss indicating a non-linear response; Mod_cont specifies that the model only contained a linear term of BA loss indicating a linear response; and Modnull1 specifies that the model indicated little or no change over the gradient of BA loss.

Potentially mineralisable nitrogen of the organic layer	Modnull1	Null model	3	-122.24	250.909	0	0.461	0	No
	Mod_cont_NL	BA decline + BA decline^2	5	-120.25	251.611	0.702	0.325	0.001	
	Mod_cont	BA decline	4	-121.86	252.438	1.529	0.215	0.001	
Potentially mineralisable nitrogen of the mineral layer	Mod_cont_NL	BA decline + BA decline^2 + soil moisture	6	-186.84	387.27	0	0.974	0.129	No
	Mod_cont	BA decline	5	-191.74	394.586	7.317	0.025	0.091	
		+ soil moisture							
	Modnull1	Null model	4	-196.92	402.558	15.289	0	0.014	
Understorey biomass	Mod_cont_NL	BA decline + BA decline^2	6	-137.21	288.01	0	0.905	0.38	Yes
	Mod_cont	BA decline	5	-141.355	293.82	5.81	0.05	0.342	
	Modnull1	Null model	4	-142.626	293.98	5.97	0.046	0.335	

Response variable	Name	Model structure	df	Log likelihood	AICc	ΔAICc	AICc weight	Marginal r^2	Threshold?
Ectomycorrhizal fungi species richness	Mod_cont_NL	BA decline + BA decline^2	4	-149.4	307.526	0	0.984	0.568	Yes
	Mod_cont	BA decline	3	-154.7	315.824	8.298	0.016	0.463	
	Modnull1	Null model	2	-185.13	374.476	66.949	0	0	
Sward height	Mod_cont_NL	BA decline + BA decline^2	5	-264.5	540.106	0	1	0.507	Yes
	Mod_cont	BA decline	4	-274.56	557.849	17.743	0	0.416	
	Modnull1	Null model	3	-294.11	594.648	54.542	0	0	
Abundance of holly seedlings	Mod_cont_NL	BA decline + BA decline^2 + log(Dung)	5	-1332.8	2676.8	0	1	0.119	No
	Mod_cont	BA decline + log(Dung)	4	-1844.6	3697.83	1021.03	0	0.047	
	Modnull1	Null model	3	-1891.8	3790.04	1113.25	0	0.007	
Abundance of beech seedlings	Mod_cont_NL	BA decline + BA decline^2 + log(Dung)	5	-275.66	562.439	0	1	0.216	Yes
	Mod_cont	BA decline + log(Dung)	4	-297.96	604.637	42.198	0	0.169	
	Modnull1	Null model	3	-331.09	668.61	106.172	0	0.015	
Abundance of oak seedlings	Mod_cont_NL	BA decline + BA decline^2 + log(Dung)	5	-50.194	111.499	0	0.998	0.455	Yes
	Mod_cont	BA decline + log(Dung)	4	-57.726	124.178	12.679	0.002	0.176	
	Modnull1	Null model	3	-62.773	131.974	20.474	0	0.035	
Abundance of tree seedlings	Mod_cont_NL	BA decline + BA decline^2 + log(Dung)	5	-1372.8	2756.79	0	1	0.134	No
	Mod_cont	BA decline + log(Dung)	4	-1902.9	3814.57	1057.78	0	0.051	
	Modnull1	Null model	3	-1967.1	3940.64	1183.85	0	0.001	
Abundance of palatable seedlings	Mod_cont_NL	BA decline + BA decline^2 + log(Dung)	5	-265.39	541.9	0	1	0.294	Yes
	Mod_cont	BA decline + log(Dung)	4	-294.34	597.407	55.507	0	0.226	
	Modnull1	Null model	3	-332.49	671.411	129.511	0	0.004	
Bulk density of the soil	Modnull1	Null model	3	17.94	-29.452	0	0.828	0	No
	Mod_cont	BA decline	4	17.35	-25.973	3.479	0.145	0.033	
	Mod_cont_NL	BA decline + BA decline^2	5	16.84	-22.568	6.883	0.027	0.038	
Depth of the organic layer	Modnull1	Null model	3	-26.75	59.929	0	0.74	0	No
	Mod_cont	BA decline	4	-27.262	63.251	3.322	0.141	0.016	
	Mod_cont_NL	BA decline + BA decline^2	5	-26.234	63.58	3.651	0.119	0.038	
Average diameter at breast height of beech trees	Mod_cont_NL	BA decline + BA decline^2	5	-182.94	377.303	0	0.949	0.007	No
	Mod_cont	BA decline	4	-187.3	383.531	6.228	0.042	0.003	
	Modnull1	Null model	3	-190.1	386.737	9.434	0.008	0	

Average height of beech trees	Mod_cont_NL	BA decline + BA decline^2	5	-150.09	311.599	0	0.907	0.046	No
	Mod_cont	BA decline	4	-153.72	316.376	4.777	0.083	0.044	
	Modnull1	Null model	3	-157.01	320.567	8.968	0.01	0	
Volume of standing deadwood in a plot	Mod_cont_NL	BA decline + BA decline^2	5	-606.23	1223.58	0	1	0.043	No
	Mod_cont	BA decline	4	-616.5	1241.73	18.148	0	0.042	
	Modnull1	Null model	3	-627	1260.42	36.843	0	0	
Volume of lying deadwood in a plot	Mod_cont_NL	BA decline + BA decline^2	5	-74.148	159.407	0	0.548	0.448	No
	Mod_cont	BA decline	4	-75.534	159.796	0.388	0.452	0.443	
	Modnull1	Null model	3	-93.483	193.394	33.987	0	0	
C/N ratio of the soil	Mod_cont_NL	BA decline + BA decline^2 + pH	5	-154.33	319.77	0	0.775	0.06	No
	Mod_cont	BA decline + pH	4	-156.8	322.325	2.555	0.216	0.056	
	Modnull1	Null model	3	-161.11	328.647	8.877	0.009	0	
Potassium exchangeable cations concentration in the mineral layer soil	Modnull1	Null model	3	76.59	-146.75	0	0.513	0.199	No
	Mod_cont	BA decline + pH	4	77.626	-146.53	0.225	0.458	0.317	
	Mod_cont_NL	BA decline + BA decline^2 + pH	5	76.036	-140.96	5.791	0.028	0.316	
Magnesium exchangeable cations concentration in the mineral layer soil	Mod_cont_NL	BA decline + BA decline^2 + pH	5	-105.07	223.724	0	0.546	0.035	No
	Mod_cont	BA decline + pH	5	-106.55	224.22	0.495	0.426	0.035	
	Modnull1	Null model	3	-111.6	229.631	5.907	0.028	0	
Sodium exchangeable cations concentration in the mineral layer soil	Mod_cont	BA decline + pH	4	110.275	-209.44	0	0.969	0.335	No
	Mod_cont_NL	BA decline + BA decline^2 + pH	5	107.98	-202.38	7.063	0.028	0.332	
	Modnull1	Null model	3	102.076	-197.72	11.715	0.003	0	
Calcium exchangeable cations concentration in the mineral layer soil	Mod_cont	BA decline + pH	4	17.362	-23.612	0	0.845	0.175	No
	Mod_cont_NL	BA decline + BA decline^2 + pH	5	16.642	-19.699	3.914	0.119	0.173	
	Modnull1	Null model	3	11.842	-17.256	6.356	0.035	0	
Manganese exchangeable cations concentration in the mineral layer soil	Modnull1	Null model	3	88.883	-171.34	0	0.983	0.065	No
	Mod_cont	BA decline + pH	5	85.913	-163.1	8.238	0.016	0.065	
	Mod_cont_NL	BA decline + BA decline^2 + pH	5	84.722	-158.33	13.006	0.001	0.085	
Iron exchangeable cations concentration in the mineral layer soil	Mod_cont_NL	BA decline + BA decline^2 + pH	5	-268.34	547.793	0	0.974	0.085	No
	Mod_cont	BA decline + pH	4	-273.18	555.087	7.294	0.025	0.072	
	Modnull1	Null model	3	-279.19	564.801	17.008	0	0	

Aluminium exchangeable cations concentration in the mineral layer soil	Modnull1	Null model	3	-38.524	83.476	0	0.511	0	No
	Mod_cont	BA decline + pH	4	-37.721	84.169	0.693	0.362	0.031	
	Mod_cont_NL	BA decline + BA decline^2 + pH	5	-37.576	86.262	2.786	0.127	0.031	
Availability of soil phosphorus	Modnull1	Null model	3	72.697	-138.97	0	0.982	0	No
	Mod_cont	BA decline + pH	4	69.793	-130.86	8.108	0.017	0	
	Mod_cont_NL	BA decline + BA decline^2 + pH	5	68.117	-125.12	13.844	0.001	0	
Total soil nitrogen	Modnull1	Null model	3	-61.364	129.156	0	0.931	0	No
	Mod_cont	BA decline + pH	5	-62.091	135.293	6.137	0.043	0.007	
	Mod_cont_NL	BA decline + BA decline^2 + pH	6	-61.363	136.312	7.156	0.026	0.009	
Total soil carbon	Mod_cont_NL	BA decline + BA decline^2 + pH	6	-228.01	469.603	0	0.943	0.076	No
	Mod_cont	BA decline + pH	5	-232.05	475.208	5.605	0.057	0.068	
	Modnull1	Null model	3	-240.08	486.589	16.986	0	0	
Soil pH	Modnull1	Null model	3	-16.753	39.934	0	0.853	0	No
	Mod_cont_NL	BA decline + BA decline^2	5	-16.862	44.835	4.901	0.074	0.037	
	Mod_cont	BA decline	4	-18.058	44.844	4.909	0.073	0	
Electrical conductivity	Modnull1	Null model	3	219.607	-432.79	0	0.996	0.105	No
	Mod_cont	BA decline	4	215.273	-421.82	10.966	0.004	0.136	
	Mod_cont_NL	BA decline + BA decline^2	5	213.517	-415.92	16.863	0	0.213	
Net ammonification	Modnull1	Null model	3	-88.247	182.964	0	0.484	0.047	No
	Mod_cont_NL	BA decline + BA decline^2	5	-86.432	184.088	1.125	0.276	0.052	
	Mod_cont	BA decline	4	-87.779	184.358	1.394	0.241	0.057	
Net nitrification	Mod_cont_NL	BA decline + BA decline^2	5	-90.104	191.433	0	0.531	0.104	No
	Mod_cont	BA decline	4	-91.485	191.77	0.337	0.449	0.103	
	Modnull1	Null model	3	-95.775	198.02	6.587	0.02	0	
Net mineralisation	Mod_cont_NL2	BA decline + BA decline^2 + pH	6	-118.42	250.589	0	0.532	0.069	No
	Mod_cont2	BA decline + pH	5	-120.62	252.466	1.877	0.208	0.064	
	Mod_cont_NL	BA decline + BA decline^2	5	-120.97	253.168	2.579	0.147	0.065	
	Mod_cont	BA decline	4	-123.25	255.303	4.715	0.05	0.056	
	Modnull1	Null model	3	-125.97	258.414	7.825	0.011	0	
Soil respiration rate	Mod_cont_NL	BA decline + BA decline^2	5	-80.996	173.1	0	0.684	0.155	Yes
	Mod_cont	BA decline	4	-84.043	176.8	3.71	0.216	0.103	
	Modnull1	Null model	3	-87.376	181.2	8.08	0.1	0	

Soil temperature	Mod_cont_NL	BA decline + BA decline^2	5	-99.623	210.356	0	0.739	0.136	No
	Mod_cont	BA decline	4	-101.86	212.443	2.087	0.26	0.122	
	Modnull1	Null model	3	-108.71	223.845	13.488	0.001	0	
Total stand carbon (vegetation, deadwood and soil)	Mod_cont	BA decline	4	266.419	-524.11	0	0.639	0.501	No
	Mod_cont_NL	BA decline + BA decline^2	5	267.038	-522.97	1.145	0.361	0.584	
	Modnull1	Null model	3	251.796	-497.16	26.946	0	0	
Aboveground biomass	Mod_cont	BA decline	4	-340.95	690.621	8.496	0.014	0.537	No
	Mod_cont_NL	BA decline + BA decline^2	5	-335.51	682.124	0	0.986	0.534	
	Modnull1	Null model	3	-372.15	750.723	68.599	0	0	
Soil clay percentage	Modnull1	Null model	3	-16.773	39.975	0	0.896	0	No
	Mod_cont	BA decline	4	-18.002	44.73	4.756	0.083	0.003	
	Mod_cont_NL	BA decline + BA decline^2	5	-18.164	47.439	7.465	0.021	0.004	
Soil silt percentage	Modnull1	Null model	3	2.618	1.193	0	0.718	0	No
	Mod_cont	BA decline	4	2.658	3.411	2.218	0.237	0.043	
	Mod_cont_NL	BA decline + BA decline^2	5	2.195	6.721	5.528	0.045	0.043	
Soil sand percentage	Modnull1	Null model	3	-20.488	47.404	0	0.823	0	No
	Mod_cont	BA decline	4	-21.116	50.958	3.554	0.139	0.014	
	Mod_cont_NL	BA decline + BA decline^2	5	-21.213	53.536	6.133	0.038	0.014	
Bracken cover	Mod_cont_NL	BA decline + BA decline^2	5	-137.02	285.155	0	0.711	0.245	No
	Mod_cont	BA decline	4	-139.11	286.952	1.797	0.289	0.245	
	Modnull1	Null model	3	-150.3	307.035	21.88	0	0	
Bare ground and moss cover	Mod_cont_NL	BA decline + BA decline^2	5	-101.16	213.425	0	0.769	0.199	No
	Mod_cont	BA decline	4	-103.56	215.847	2.422	0.229	0.175	
	Modnull1	Null model	3	-109.54	225.517	12.092	0.002	0	
Litter cover	Mod_cont_NL	BA decline + BA decline^2	5	-119.17	249.446	0	0.718	0.646	No
	Mod_cont	BA decline	4	-121.3	251.319	1.873	0.282	0.645	
	Modnull1	Null model	3	-159.07	324.574	75.129	0	0	
Grass cover	Mod_cont	BA decline	4	9.434	-10.14	0	0.819	0.161	No
	Mod_cont_NL	BA decline + BA decline^2	5	9.08	-7.049	3.091	0.175	0.164	
	Modnull1	Null model	3	3.389	-0.35	9.79	0.006	0	

Palatable tree browseline	Mod_cont_NL	BA decline + BA decline^2	5	-94.72	200.979	0	0.556	0.028	No
	Mod_cont	BA decline	4	-96.76	202.519	1.541	0.257	0.028	
	Modnull1	Null model	3	-98.285	203.155	2.176	0.187	0	
Unpalatable tree browseline	Mod_cont_NL	BA decline + BA decline^2	5	-112.05	235.38	0	0.602	0.035	No
	Mod_cont	BA decline	4	-114.08	237.002	1.622	0.268	0.031	
	Modnull1	Null model	3	-115.98	238.449	3.069	0.13	0	
Holly cover	Modnull1	Null model	3	-66.398	139.445	0	0.471	0	No
	Mod_cont_NL	BA decline + BA decline^2	5	-64.272	140.258	0.813	0.313	0.005	
	Mod_cont	BA decline	4	-65.945	141.002	1.557	0.216	0.002	
Rubus cover	Mod_cont_NL	BA decline + BA decline^2	5	-71.326	154.366	0	0.622	0.184	No
	Mod_cont	BA decline	4	-73.14	155.391	1.025	0.373	0.188	
	Modnull1	Null model	3	-78.591	163.832	9.466	0.005	0	
Holly shrubs browsed	Modnull1	Null model	3	-58.867	124.163	0	0.407	0	No
	Mod_cont	BA decline	4	-57.975	124.677	0.514	0.315	0.047	
	Mod_cont_NL	BA decline + BA decline^2	5	-56.907	124.926	0.763	0.278	0.059	
Rubus shrubs browsed	Mod_cont_NL	BA decline + BA decline^2	5	-73.077	157.868	0	0.831	0.129	No
	Mod_cont	BA decline	4	-76.25	161.611	3.744	0.128	0.076	
	Modnull1	Null model	3	-78.612	163.873	6.005	0.041	0	
Average crown condition	Mod_cont	BA decline	4	9.554	-10.177	0	0.639	0.156	No
	Mod_cont_NL	BA decline + BA decline^2	5	9.691	-7.954	2.224	0.21	0.155	
	Modnull1	Null model	3	6.921	-7.296	2.881	0.151	0	
Understorey condition	Modnull1	Null model	3	-19.867	46.35	0	0.829	0	No
	Mod_cont	BA decline	4	-20.713	50.478	4.128	0.105	0.004	
	Mod_cont_NL	BA decline + BA decline^2	5	-19.898	51.418	5.068	0.066	0.028	
Canopy openness	Mod_cont_NL	BA decline + BA decline^2	5	-43.877	98.866	0	0.988	0.886	Yes
	Mod_cont	BA decline	4	-49.514	107.756	8.89	0.012	0.872	
	Modnull1	Null model	3	-112.8	232.025	133.159	0	0	
Understorey openness	Mod_cont_NL	BA decline + BA decline^2	5	-115.73	242.573	0	0.602	0.292	No
	Mod_cont	BA decline	4	-117.34	243.401	0.828	0.398	0.295	
	Modnull1	Null model	3	-130.79	268.004	25.431	0	0	
Tree seedling richness	Mod_cont	BA decline	3	-102.42	211.273	0	0.732	0.195	No
	Mod_cont_NL	BA decline + BA decline^2	4	-102.29	213.301	2.028	0.265	0.209	
	Modnull1	Null model	2	-109.1	222.414	11.141	0.003	0	
Tree sapling richness	Modnull1	Null model	2	-62.582	129.375	0	0.693	0	No
	Mod_cont	BA decline	3	-62.561	131.551	2.176	0.233	0.001	
	Mod_cont_NL	BA decline + BA decline^2	4	-62.561	133.85	4.475	0.074	0.001	

Spider species richness	Mod_cont	BA decline	3	-55.813	118.769	0	0.496	0.138	No
	Modnull1	Null model	2	-57.636	119.817	1.048	0.294	0	
	Mod_cont_NL	BA decline + BA decline^2	4	-55.245	120.49	1.721	0.21	0.189	
Rove beetles species richness	Modnull1	Null model	2	-50.365	105.276	0	0.595	0	No
	Mod_cont_NL	BA decline + BA decline^2	4	-48.635	107.27	1.994	0.22	0.134	
	Mod_cont	BA decline	3	-50.232	107.607	2.331	0.185	0.012	
Carabid beetles species richness	Modnull1	Null model	2	-51.53	107.606	0	0.614	0	No
	Mod_cont	BA decline	3	-51.005	109.153	1.547	0.283	0.046	
	Mod_cont_NL	BA decline + BA decline^2	4	-50.59	111.179	3.573	0.103	0.086	
Ant species richness	Mod_cont	BA decline	3	-37.656	82.455	0	0.775	0.484	No
	Mod_cont_NL	BA decline	4	-37.467	84.933	2.479	0.224	0.529	
	Modnull1	Null model	2	-45.428	95.401	12.946	0.001	0	
Weevil species richness	Modnull1	Null model	2	-28.533	61.611	0	0.724	0	No
	Mod_cont	BA decline	3	-28.485	64.113	2.502	0.207	0.006	
	Mod_cont_NL	BA decline + BA decline^2	4	-28.165	66.33	4.719	0.068	0.048	
Woodlice species richness	Modnull1	Null model	2	-37.242	79.029	0	0.732	0	No
	Mod_cont	BA decline	3	-37.226	81.595	2.566	0.203	0.002	
	Mod_cont_NL	BA decline + BA decline^2	4	-36.943	83.887	4.857	0.065	0.029	
Ground-dwelling arthropod species richness	Mod_cont	BA decline	3	-69.5	146.15	0	0.74	0.264	No
	Mod_cont_NL	BA decline + BA decline^2	4	-69.28	148.56	2.41	0.22	0.283	
		+ BA decline^2							
	Modnull1	Null model	2	-73.72	151.98	5.84	0.04	0	
Moisture content of the mineral layer	Mod_cont_NL	BA decline + BA decline^2	5	-208.68	428.469	0	0.909	0.026	No
	Mod_cont	BA decline	4	-212.41	433.539	5.07	0.072	0.013	
	Modnull1	Null model	3	-214.89	436.202	7.733	0.019	0	
Moisture content of the organic layer	Mod_cont_NL	BA decline + BA decline^2	5	-300.81	612.734	0	0.971	0.005	No
	Mod_cont	BA decline	4	-305.58	619.878	7.143	0.027	0.005	
	Modnull1	Null model	3	-309.38	625.194	12.46	0.002	0	
Cervus dung proportional	Mod_cont_NL	BA decline + BA decline^2	4	-2758.3	5525.3	0	1	0.029	No
	Mod_cont	BA decline	3	-2780.3	5567.07	41.766	0	0.001	
	Modnull1	Null model	2	-2871.2	5746.54	221.241	0	0	

Equus dung proportional	Mod_cont	BA decline	3	-627.11	1260.65	0	0.759	0.173	
	Mod_cont_NL	BA decline + BA decline^2	4	-627.11	1262.95	2.298	0.241	0.175	No
	Modnull1	Null model	2	-729.68	1463.57	202.92	0	0	
Proportional dung total	Mod_cont_NL	BA decline + BA decline^2	4	-2636.6	5281.92	0	1	0.016	No
	Mod_cont	BA decline	3	-2647.1	5300.56	18.636	0	0.004	
	Modnull1	Null model	2	-2674.3	5352.8	70.88	0	0	
Very large beech trees (74.97 cm < dbh < 103 cm)	Mod_cont	BA decline	3	-61.549	129.643	0	0.586	0.104	
	Modnull1	Null model	2	-63.607	131.48	1.836	0.234	0	
	Mod_cont_NL	BA decline + BA decline^2	4	-61.535	132	2.356	0.18	0.101	No
Large beech trees (68.32 cm < dbh < 74.97 cm)	Mod_cont	BA decline	3	-59.977	126.499	0	0.744	0.294	
	Mod_cont_NL	BA decline + BA decline^2	4	-59.857	128.644	2.145	0.255	0.322	No
	Modnull1	Null model	2	-67.724	139.714	13.216	0.001	0	
Holly tree abundance	Mod_cont	BA decline	3	-118.51	243.555	0	0.454	0.015	
	Mod_cont_NL	BA decline + BA decline^2	4	-117.8	244.532	0.978	0.279	0.019	No
	Modnull1	Null model	2	-120.17	244.615	1.06	0.267	0	
Beech trees abundance	Mod_cont_NL	BA decline + BA decline^2	4	-101	210.719	0	1	0.778	
	Mod_cont	BA decline	3	-111.49	229.4	18.682	0	0.639	Yes
	Modnull1	Null model	2	-171.05	346.306	135.587	0	0	
Holly saplings abundance	Mod_cont_NL	BA decline + BA decline^2	4	-354.54	717.797	0	0.988	0.005	
	Mod_cont	BA decline	3	-360.28	726.991	9.195	0.01	0	No
	Modnull1	Null model	2	-363.17	730.549	12.752	0.002	0	
Beech saplings abundance	Mod_cont_NL	BA decline + BA decline^2	4	-35.653	80.033	0	0.997	0.075	
	Mod_cont	BA decline	3	-42.921	92.27	12.236	0.002	0.008	No
	Modnull1	Null model	2	-44.862	93.935	13.902	0.001	0	
Overall saplings abundance	Mod_cont_NL	BA decline + BA decline^2	4	-369.57	747.876	0	0.95	0.006	
	Mod_cont	BA decline	3	-373.97	754.369	6.493	0.037	0	No
	Modnull1	Null model	2	-376.15	756.504	8.628	0.013	0	
Ground flora species richness	Mod_cont_NL	BA decline + BA decline^2 + log(Dung)	5	-183.09	377.285	0	0.898	0.596	
	Mod_cont	BA decline + log(Dung)	4	-186.96	382.653	5.368	0.061	0.548	Yes
	Mod_cont_NL2	BA decline + BA decline^2	4	-187.4	383.531	6.246	0.04	0.549	
	Mod_cont2	BA decline	3	-192.55	391.533	14.249	0.001	0.486	
	Modnull1	Null model	3	-257.45	521.336	144.052	0	0.028	
Woody ground flora species richness	Mod_cont2	BA decline	3	-112.51	231.446	0	0.494	0.052	
	Mod_cont	BA decline + log(Dung)	4	-112.4	233.532	2.087	0.174	0.055	
	Mod_cont_NL2	BA decline + BA decline^2	4	-112.5	233.731	2.285	0.158	0.053	No
	Modnull1	Null model	3	-113.92	234.265	2.819	0.121	0.001	
	Mod_cont_NL	BA decline + BA decline^2 + log(Dung)	5	-112.4	235.912	4.467	0.053	0.056	

Non-woody ground flora species richness	Mod_cont_NL	BA decline + BA decline^2 + log(Dung)	5	-172.81	356.738	0	0.956	0.655	Yes
	Mod_cont_NL2	BA decline + BA decline^2	4	-177.13	362.98	6.242	0.042	0.61	
	Mod_cont	BA decline + log(Dung)	4	-180.15	369.033	12.295	0.002	0.582	
	Mod_cont2	BA decline	3	-186.09	378.598	21.86	0	0.517	
	Modnull1	Null model	3	-262.04	530.507	173.769	0	0.032	
Lichen species richness	Mod_cont_NL	BA decline + BA decline^2 + Holly abundance	5	-221.1	453.317	0	1	0.437	Yes
	Mod_cont	BA decline + Holly abundance	4	-231.85	472.417	19.1	0	0.331	
	Modnull1	Null model	3	-250.11	506.652	53.335	0	0.14	
Lichen species richness on holly	Modnull1	Null model	2	-224.964	454.138	0	0.498	0	No
	Mod_cont	BA decline	3	-224.168	454.764	0.626	0.364	0.001	
	Mod_cont_NL	BA decline + BA decline^2	4	-223.993	456.712	2.574	0.138	0.004	
Lichen species richness on beech	Mod_cont_NL	BA decline + BA decline^2	4	-208.98	426.688	0	1	0.599	Yes
	Mod_cont	BA decline	3	-238.79	484.014	57.326	0	0.392	
	Modnull1	Null model	2	-289.57	583.34	156.652	0	0	
Organic layer loss on ignition	Modnull1	Null model	3	-47.462	101.352	0	0.735	0	No
	Mod_cont	BA decline	4	-47.661	104.049	2.697	0.191	0.008	
	Mod_cont_NL	BA decline + BA decline^2	5	-47.408	105.927	4.575	0.075	0.008	
Mineral layer loss on ignition	Modnull1	Null model	3	-63.385	133.199	0	0.52	0	No
	Mod_cont	BA decline	4	-62.741	134.209	1.01	0.314	0.02	
	Mod_cont_NL	BA decline + BA decline^2	5	-62.18	135.47	2.271	0.167	0.02	
Organic layer nitrate concentration	Modnull1	Null model	3	-63.091	132.611	0	0.399	0	No
	Mod_cont_NL	BA decline + BA decline^2	5	-60.917	132.946	0.335	0.338	0.054	
	Mod_cont	BA decline	4	-62.359	133.446	0.835	0.263	0.034	
Mineral layer nitrate concentration	Modnull1	Null model	3	-63.091	132.611	0	0.399	0	No
	Mod_cont_NL	BA decline	5	-60.917	132.946	0.335	0.338	0.054	
		BA decline + BA decline^2							
Organic layer ammonium concentration	Mod_cont_NL	BA decline + BA decline^2	5	-235.07	481.246	0	0.959	0.052	No
	Mod_cont	BA decline	4	-239.47	487.665	6.419	0.039	0.036	
	Modnull1	Null model	3	-243.47	493.374	12.128	0.002	0	
Mineral layer ammonium concentration	Modnull1	Null model	3	-43.781	93.99	0	0.776	0	No
	Mod_cont	BA decline	4	-44.375	97.477	3.487	0.136	0.003	
	Mod_cont_NL	BA decline + BA decline^2	5	-43.62	98.351	4.361	0.088	0.006	

Appendix 2.5: 'Thresholds of biodiversity and ecosystem function in a forest ecosystem undergoing dieback', the published version of Chapter 2.

Thresholds of biodiversity and ecosystem function in a forest ecosystem undergoing dieback

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Ecological thresholds, which represent points of rapid change in ecological properties, are of major scientific and societal concern. However, very little research has focused on empirically testing the occurrence of thresholds in temperate terrestrial ecosystems. To address this knowledge gap, we tested whether a number of biodiversity, ecosystem functions and ecosystem condition metrics exhibited thresholds in response to a gradient of forest dieback, measured as changes in basal area of living trees relative to areas that lacked recent dieback. The gradient of dieback was sampled using 12 replicate study areas in a temperate forest ecosystem. Our results provide novel evidence of several thresholds in biodiversity (namely species richness of ectomycorrhizal fungi, epiphytic lichen and ground flora); for ecological condition (e.g. sward height, palatable seedling abundance) and a single threshold for ecosystem function (i.e. soil respiration rate). Mechanisms for these thresholds are explored. As climate-induced forest dieback is increasing worldwide, both in scale and speed, these results imply that threshold responses may become increasingly widespread.

The living world is currently experiencing an unprecedented period of environmental change[1–4]. In recent decades, human-derived actions such as carbon emission, introduction of species and large-scale land transformations (e.g. urban and agricultural expansion) have become pervasive throughout the biosphere. Impacts of human activity have become so widespread and intrusive that a new geological epoch, the Anthropocene, has been proposed[5]. Human actions have influenced the functioning of the Earth system to such an

extent that the consequences could be detrimental or even catastrophic for human society[1–4]. This is reflected in development of the planetary boundaries concept, which suggests that if specific thresholds of environmental change are transgressed, there may be increased risks to human wellbeing or to resilience of the whole Earth system[2, 3].

The concept of planetary boundaries, together with allied concepts such as resilience[2, 3], depends on the existence of ecological thresholds. Such thresholds are defined as points or zones where relatively rapid change occurs from one ecological condition to another[6], and are characterised by a non-linear response of an ecosystem property to a controlling variable that increases linearly[7]. If thresholds occur in nature, a slight increase in disturbance intensity or frequency could cause a disproportionate change in an ecosystem property. Such changes could include the loss of biodiversity crucial for ecosystem function[8] and the loss of regulatory ecosystem services on which humans depend[9]. Moreover, a threshold in one ecosystem property could sequentially disrupt the self-organising networks that govern local dynamics of other systems[10], and could potentially cause unpredictable responses at the scale of whole Earth system dynamics[3, 6, 11]. There is a need to avoid crossing such thresholds to enable ecological systems, and their associated socio-economic systems, to be maintained in the future[12].

Ecological thresholds are thought to be attributable to shifts in the relative strength of balancing (i.e. negative) and reinforcing (i.e. positive) feedback loops that influence the dynamics of an ecosystem[13]. For example, in many terrestrial ecosystems, low water availability acts to regulate the growth of plants. Conversely, if water availability increases by a sufficient amount, the biomass and complexity of vegetation can increase, which can further increase water availability by modifying the water cycle[14, 15].

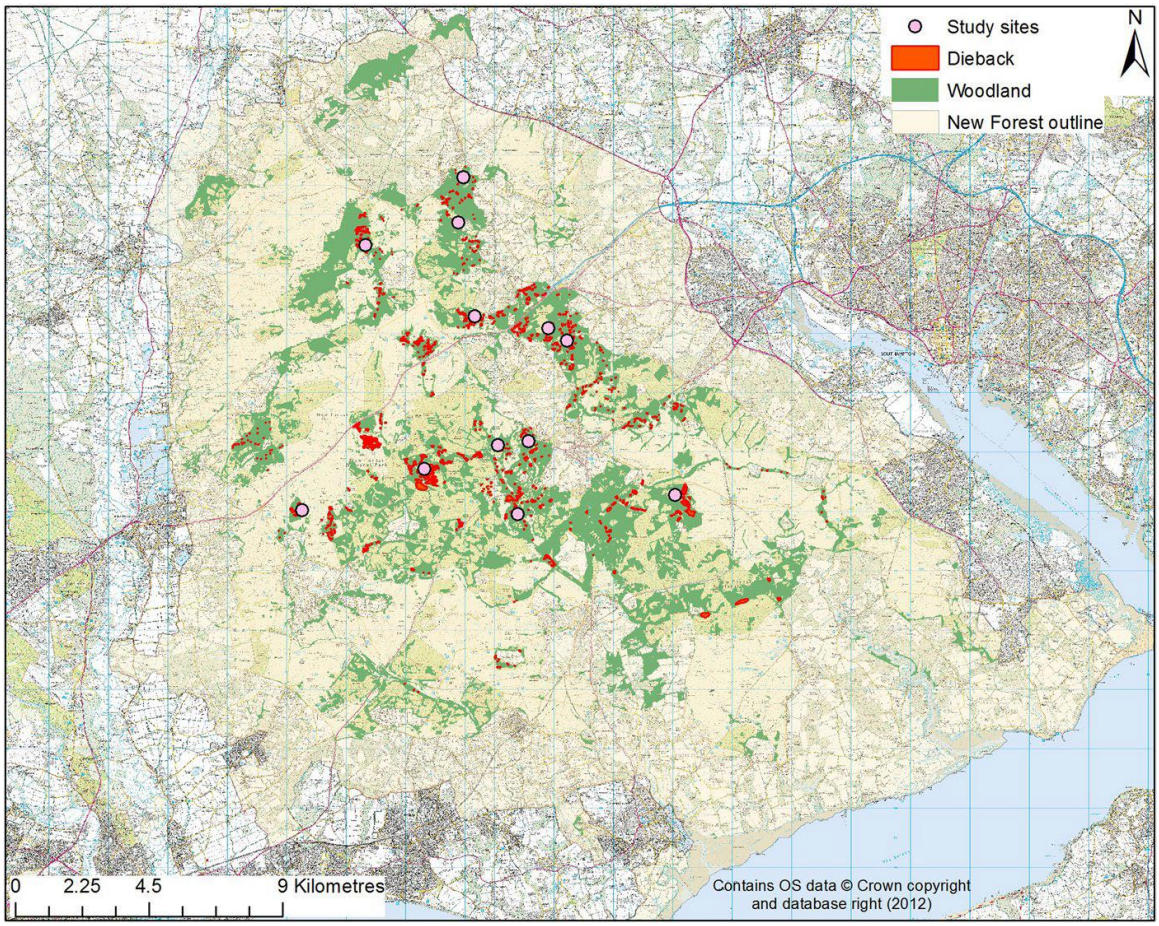

Figure 1. Distribution of broadleaved woodland (green), occurrence of dieback (red) and location of each of the 12 study areas (pink dots) in the New Forest, in southern England. Map was made using ArcMap 10.1 (http://desktop.arcgis.com/en/arcmap/).

Despite the perceived global importance of ecological thresholds, supporting evidence is largely theoretical[7, 16], and the issue is the focus of major scientific debate[17, 18]. Supporting empirical evidence from field situations is severely limited[6, 19], and is primarily available for aquatic systems[20–22]. Field evidence for ecological thresholds resulting from environmental change is particularly lacking in temperate woodland ecosystems that are not governed by fire[6, 23]. This research therefore aimed to test the hypothesis that threshold responses exist in measures of (1) biodiversity, (2) ecosystem function and (3) ecosystem condition within a terrestrial ecosystem, specifically temperate forest. To test this hypothesis, we examined a beech-dominated forest that is currently undergoing large-scale dieback in response to environmental change, as revealed through analysis of long-term monitoring data[24].

Methods

Study area. We carried out this study in the New Forest National Park (NP), which covers an area of 57,100 ha situated in southern England (longitude: 1°17′59″ to 1°48′8″ W, Latitude: 50°42′19″ to 51°0′17″ N) (Fig. 1). The Forest consists of a mosaic of heathland, mire, grassland and coniferous and broadleaf woodland (8,472 ha) ecosystems. These woodlands are dominated by beech (*Fagus sylvatica*), often occurring with oak (*Quercus robur*) and birch (*Betula pendula*), and typically with holly (*Ilex aquifolium*) in the understorey[25]. The local climate is oceanic and temperate, with a mean annual maximum temperature of 14.8 °C and annual rainfall of 835.2 mm, based on data available between 1981 and 2010[26]. The Park contains the largest area of semi-natural vegetation in lowland Britain[27, 28], and is of exceptional importance for biodiversity conservation[29]. The New Forest is also characterised by high densities of large herbivores, including livestock and deer, reflecting its history as a Royal hunting reserve[27].

Experimental design. A geographic information system (GIS) (ArcGIS 10.1) was utilised to identify suitable study sites of forest dieback within the New Forest. Spatial information included 25 cm resolution aerial photographs, captured in 2007 by GeoPerspectives, and areas of known historic woodland dieback, recorded in 1999[30]. The resulting areas of dieback were overlaid on top of several layers, including soil data (NATMAP; National Soil Map), obtained from National Soil Resources Institute (NSRI), Silsoe, Bedfordshire, UK; regeneration plots; and a tree composition map, derived from data collected in 1982[31]. Twelve sites where recent dieback of mature native broadleaf woodland has been observed[32] were selected for study. Within each site, five 20 × 20 m survey plots were established to provide a gradient of woodland dieback, using basal area (BA) as a measure of forest structure, calculated following Cantarello and Newton[33]. In each case, beech was the dominant canopy tree species. Plots were situated to provide values of 100%, 75%, 50%, 25% and 0% BA (see Supplementary Information Fig. S1 and Table S1), with 100% representing an intact forest stand and 0% indicating complete death of all canopy trees, identified by the presence of standing deadwood. Secondary criteria required canopy openness due to canopy death to increase positively with dieback stage, and that plots other than the intact stage plots had standing or lying deadwood present. The five stages were: (1) intact (no dieback); (2) slight dieback; (3) moderate dieback; (4) major dieback; and (5) total dieback. The mean of the 12 intact plots was used as a baseline value. In this way, in each of the 12 study sites, one plot was sampled in each of the five basal area classes. This design represents a form of space-for-time

substitution, for which spatial variation in BA was assumed to represent temporal dieback of the forest stands.

Plot set-up. Each plot was 20 × 20 m (400 m^2; 0.04 ha). A nested sub-plot of 10 × 10 m (100 m^2) was set up in the centre of each plot, laid out in the same orientation as the full plot. The centre and the corners of the sub-plot were marked with wooden stakes for easy identification on return visits. The mid-points of each plot were recorded using a handheld GPS (GPSMAP 60CSx; Garmin, USA) (see Supplementary Information SM1).

Field measurements. Within each survey plot we identified tree species and diameter at breast height (dbh, 1.3 m) were recorded. We undertook detailed surveys of each plot to identify species of epiphytic lichens, ground flora, tree saplings and seedlings and ectomycorrhizal fungi (ECM) based on the identification of sporocarps. In five sites ground-dwelling arthropods were trapped in pitfall traps and identified using DNA barcoding methods (see Supplementary Information SM2).

As soil condition and structure are important to the productivity of the whole woodland ecosystem, we sampled soils within each plot then analysed bulk density, nitrate, ammonium, potentially mineralisable nitrogen, C, K, P, S, Ca, Mg, Na, Al, Mn, pH, electrical conductivity, organic matter, soil moisture, soil temperature and particle size distribution using standard analytical procedures. We recorded *in-situ* nitrogen mineralisation and nitrification using a resin capsule (Unibest, Walla Walla, WA, USA), following DeLuca *et al.*[34] (see Supplementary Information SM1).

We made measurements of tree crown condition[35], canopy openness[36] and deadwood volume following Newton[37]. As a metric of herbivory, dung counts[38], plant browsing[39, 40] scrub layer presence and condition[41] and sward height[42] were recorded. Aboveground biomass and carbon storage were calculated following Jenkins *et al.*[43]. Soil respiration rate was measured with a portable EGM-4 Environmental Gas Monitor CO_2 infrared gas analyser (IRGA) equipped with a closed system soil respiration chamber (PP Systems, Amesbury, MA, USA) (see Supplementary Information SM1). For all variables measured, see Supplementary Information Table S2.

Data analysis. All measured variables were analysed in relation to gradients in BA, treating the twelve sites as independent replicates. As BA was scaled linearly along the gradients (see Supplementary Information Fig. S1 and Table S1), any departure from linearity provided potential evidence of a threshold response. Generalised linear mixed models

(GLMMs) were used to analyse these responses. This was achieved by fitting the most parsimonious models (determined using AICc) of the relationships between percentage BA and the response variables, using other measured predictors as fixed effects and study area as a random effect. All analyses were performed in R 3.1.2. (R Development Core Team, 2011, http://www.R-project.org) using the lme4[44] and ggplot2[45] packages for mixed models. In this study, the r_2 measure used was the marginal r_2, which describes the proportion of variance explained by the fixed effect alone[46]. A response variable was considered to show a threshold if it met three criteria relating to the most parsimonious model: (1) the model included a quadratic term; (2) its ΔAICc was ≥3 compared to the next closest model; and (3) its marginal r^2 value was >0.15. These criteria were defined *a priori*, before conducting the analysis, to ensure a degree of rigour and objectivity in our detection of threshold responses. It should be noted that the criteria were developed by ourselves, based on what we considered to be consistent with good practice. Different results may have been obtained had other criteria been adopted.

Results

Over half (44/86) of the measured variables showed non-linear responses over the dieback gradient in this study, of which 13 exhibited thresholds according to our criteria. Here we identify the most clearly defined thresholds (i.e. those associated with small confidence intervals) pertaining to biodiversity, ecosystem function and ecological condition (see Supplementary Table S2 for additional results).

Biodiversity. The relationship between ground flora species richness and dieback was best predicted by a regression model with a quadratic term of BA loss and a dung predictor term for all ground flora (r^2 = 0.60, ΔAICc = 5.37) (Fig. 2a) and for ground flora not including woody species (r^2 = 0.66, ΔAICc = 6.24). The most parsimonious ECM species richness model exhibited a threshold, with a quadratic term of BA loss (r^2 = 0.57, ΔAICc = 8.30) (Fig. 2b). In addition, total epiphytic lichen species richness exhibited a threshold response, with linear and quadratic terms of BA loss and a holly abundance term included in the most parsimonious model (r^2 = 0.44, ΔAICc = 19.1) (Fig. 2c), while lichen species richness on beech trees specifically also exhibited a threshold response (r^2 = 0.60, ΔAICc = 57.32), exhibited by having a quadratic and linear BA loss as its terms. Thresholds were not present in ground-dwelling arthropod richness, which was best represented by a linear BA term (r^2= 0.26, ΔAICc = 2.41) (see Fig. S2a) or tree seedling richness, which was also

best represented by a single linear BA term (r^2 = 0.19, ΔAICc = 2.02). Excluding the additional predictors of dung and holly abundance from ground flora and lichen analysis, respectively, all ground flora (r^2 = 0.55, ΔAICc = 8.00), ground flora not including woody species (r_2 = 0.61, ΔAICc = 15.62) and total epiphytic lichen species richness (r^2 = 0.24, ΔAICc = 12.20) were still best predicted by models with a quadratic term of BA loss, thus exhibiting thresholds (Supplementary Information, Table S4).

Ecosystem functions. Only a single threshold response was exhibited in the 27 soil function variables measured over the dieback gradient, namely the case of soil respiration rate, which was demonstrated by quadratic term of BA loss included in the most parsimonious model (r^2 = 0.16; ΔAICc = 3.71) (Fig. 2d). For other soil functions, models with non-linear terms were often the most parsimonious models; however, these displayed very low r^2 and ΔAICc values and were not therefore considered to be exhibiting thresholds. These included potentially mineralisable nitrogen in the mineral layer (r^2 = 0.07; ΔAICc = 0.53) (PMNM; see Fig. S2b) and N mineralisation (r^2 = 0.13; ΔAICc = 0.97) (see Fig. S2c). Other modelled soil function results indicated that strong linear relationships were exhibited in the exchangeable cations of Na (r^2 = 0.34; ΔAICc = 7.06) and Ca (r^2 = 0.18; ΔAICc = 3.91). Total carbon storage was best predicted by a model with solely a linear BA term (r^2 = 0.50; ΔAICc = 1.14) (see Fig. S2d). The most parsimonious models for all other soil function variables either had lower r^2 values, or were best modelled by null models.

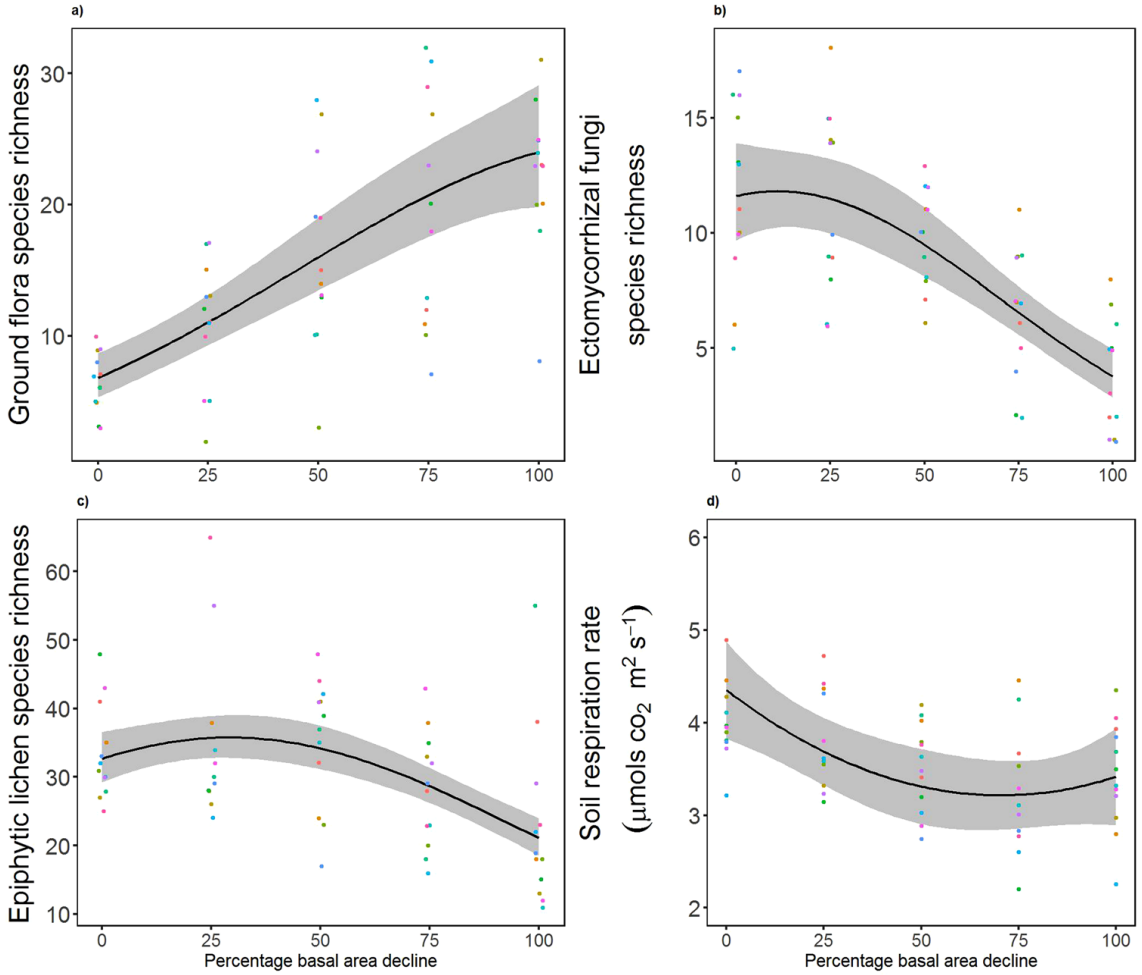

Figure 2. Threshold relationships between stage of dieback and species richness and soil respiration rate. Relationships between stage of dieback and species richness of (**a**) vascular ground flora (n = 60); (**b**) ectomycorrhizal fungi (n = 60); (**c**) epiphytic lichen (n = 60); and (**d**) soil respiration rate (n = 60). The black lines represent prediction using the most parsimonious model coefficients and grey shading the 95% confidence intervals of the coefficients (marginal r^2 = 0.60, 0.57, 0.44, and 0.16 for (**a–d**), respectively). The different coloured points represent the values at each individual site. All species richness values are the number of unique species found in 0.04 ha.

Ecological condition. A threshold response in the average sward height was defined by the most parsimonious model having a quadratic term of BA loss (r^2 = 0.51; ΔAICc = 17.74) (Fig. 3a). Similarly, some of the seedling abundances (palatable seedlings, beech and oak separately and combined) showed thresholds effects, the most pronounced of which was the abundance of palatable seedlings, which had a quadratic term of BA loss and a dung factor (r^2 = 0.29; ΔAICc = 55.51). The understorey biomass also exhibited a threshold response as determined by the most parsimonious model, with a quadratic term for BA loss (r^2 = 0.38; ΔAICc = 5.81) (Fig. 3b). The condition of the remaining crowns was best described by a linear model, with only a linear BA loss term (r^2 = 0.16; ΔAICc = 2.22).

Discussion

Our results provide novel evidence of thresholds in biodiversity, ecosystem function and ecological condition in a forest ecosystem undergoing dieback. The most striking threshold responses were observed for biodiversity, specifically in the species richness of ECM fungi and epiphytic lichens, both of which started to decline sharply with a decline in BA, and ground flora, which increased until the latter stages of the BA gradient. With respect to ecosystem function, a single threshold response was identified, namely in soil respiration rate. For ecological condition, thresholds were shown in sward height, which increased after initial decline in BA, and palatable seedling abundance, which initially increased across the gradient of stand BA, but started to decline in the late stages.

Previous research has reported a number of threshold responses in forest ecosystems as a result of deforestation and habitat fragmentation, including thresholds in forest structure[47, 48], biodiversity loss[49, 50] and ecosystem service provision[51]. Moreover, thresholds have been identified across forest-savanna-grassland gradients in tropical landscapes[52–54]. These studies all focused on the impacts of direct human-driven loss (i.e. physical removal) of forest cover or modified disturbance regimes at the landscape scale. As far as we are aware, the current study is the first to report threshold responses over a gradient of stand dieback, which represents a different form of ecosystem change than deforestation. Such dieback is increasing in response to environmental change in forests globally as a result of climate change, pest and disease attack, and increasing fire frequency[15, 55, 56]. Moreover, Allen *et al.*[57] suggest that all forests may be vulnerable to climate-induced dieback in the future. The current results suggest that many other forest ecosystems that are being affected by dieback may potentially be characterised by threshold responses to environmental change.

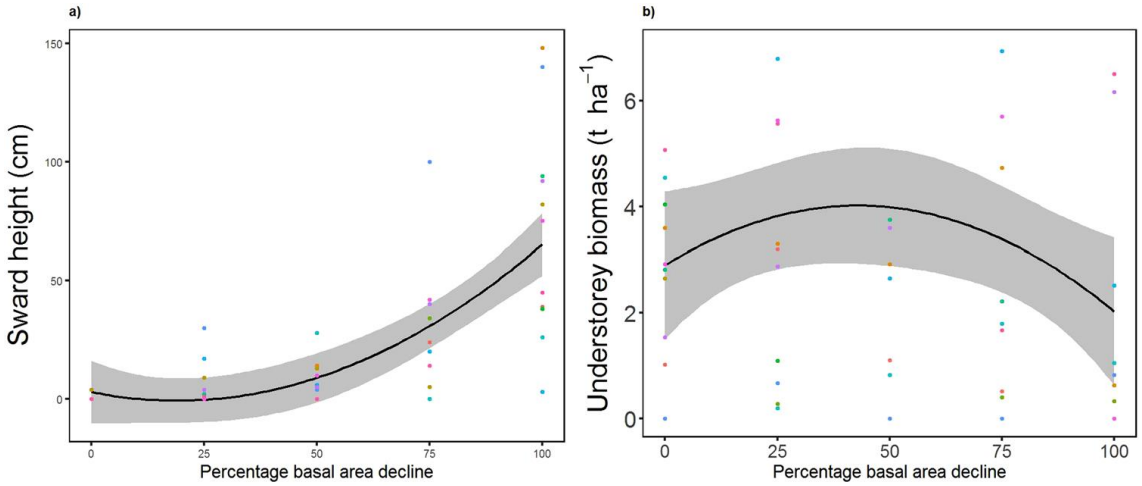

Figure 3. Threshold relationships between stage of dieback and ecosystem condition. Relationships between stage of dieback and (**a**) average sward height (n = 60); and (**b**) understorey biomass (n = 60). The black lines represent prediction using the most parsimonious model coefficients and grey shading the 95% confidence intervals of the coefficients (marginal r^2 = 0.51 and 0.38 for (**a**) and (**b**), respectively). The different coloured points represent the values at each individual site.

The basis of ecological threshold theory is that rapid, non-linear changes are observed in ecosystem 'state' as a controlling variable changes[58]. This implies that a relatively small increase in intensity or frequency of disturbance could cause rapid and abrupt declines in ecosystem condition, state or function, potentially creating highly degraded ecosystems[59, 60]. This is concerning as thresholds may compromise the capacity of forest ecosystems to recover from future perturbations[61, 62], especially as anthropogenic pressures are predicted to intensify in future[57, 63, 64].

The precise mechanisms underlying ecological thresholds remain unclear[58]. Walkers and Meyers[65] and Scheffer *et al.*[7] have highlighted that in order for a threshold to occur there must be a switch in an ecosystem from a self-regulating state (negative feedback) to one that is reinforced by further internal or external changes (positive feedback), i.e. a self-exacerbating state[66]. The thresholds we observed in our study may be the result of a number of positive feedback mechanisms including interactions between trees, soil microbes, soil chemistry and herbivory. For example, as trees die and degrade, symbiotic associations with ECM fungi are reduced[67, 68]. This can cause reductions in the abundance of other soil microorganisms owing to major modifications to water and nutrient exchanges[69–71], which could create a positive feedback that substantially lowers plant survival and growth[71, 72]. This could be evidenced by the decline in soil respiration rate that was observed in this study. In addition, the threshold observed in lichen species richness could be attributable to feedbacks between declining availability of bark substrate and changes in microclimate during the process of stand dieback[73, 74].

In contrast to biodiversity measures, relatively little evidence was obtained here of threshold responses in measures of ecosystem function. In most cases, such measures varied non-linearly with BA decline, however, they did not fulfil the ΔAICc ≥ 3 and marginal $r^2 > 0.15$ criteria. The exception was soil respiration rate, which only narrowly exceeded the marginal r_2 criterion limit ($r^2 = 0.15$). As soil respiration is a net result of the respiration of autotrophic (plant) and heterotrophic (microbial and mycorrhizal) activity[75], the initial declining trend may have been largely a result of decline in microbial activity in the soil owing to declining tree root density[76] and tree presence[77]. In all cases, our interpretation of these data was based on the assumptions underlying space-for-time substitution, which should be borne in mind when interpreting the results.

The key assumption the approach adopted here, a space-for-time substitution, is that variation detected over space accurately reflects the ecological changes occurring over time. To reduce uncertainty in this study, this assumption was tested with results obtained from a long-term monitoring investigation in the same study area undertaken by Martin *et al.*[24], which involved a beech woodland stand (Denny Wood) that has undergone stand dieback over the past 50 years. It showed that trends in BA depended on the scale at which the results were analysed; at the scale of 20 × 20 m plots (as employed in this study), BA decline was often strongly non-linear, displaying clear thresholds[24]. However, at the scale of the entire stand, BA decline was described by a linear trend. This reflects the fact that dieback of different parts of the stand was asynchronous. Of the stands that declined in BA in Denny Wood, mean values declined from 49 m_2 ha^{-1} to 23 m_2 ha^{-1} over a 50-year period[78].

A further assumption of the space-for-time substitution approach is that all other conditions are the same across the plots surveyed[34]. Fukami and Wardle[79] describe several ways to overcome this limitation. One is to include multiple sites, to uncover trends in ecosystem dynamics. In this study, 12 replicate sites were used to achieve this, with environmental condition measurements made pertaining to growing conditions and disturbance, two factors that influence woodland growth and mortality. Droughts and waterlogging events affect growth and mortality of beech[80–82], especially in southern England[30, 83], with the clay content of soil affecting how quickly water drains away. Particle size distribution analysis of soil samples from all sites demonstrated that the percent clay soil content did not change significantly ($F_{(4,55)} = 0.177$, $P = 0.949$) (Supplementary Information, Fig. S3a) across the dieback gradient, based on one-way ANOVA results. This indicated that drought or waterlogging could have had the same

effect on any plots across the dieback gradient. Other variables that could have identified the stands as having different conditions, or being of different ages all also had no significant variation over the gradient: organic soil depth ($F_{(4,55)} = 1.160$, $P = 0.338$) (Supplementary Information, Fig. S3b), which suggests that similar values of soil moisture, organic nutrients and stability were present among sites; soil pH ($F_{(4,55)} = 0.910$, $P = 0.465$) (Supplementary Information, Fig. S3c), which indicates that all the stands were similarly acidic and therefore are characterised by similar processes such as nutrient uptake that are dependent on pH; and dbh of the remaining living trees ($x_2(3) = 0.586$, $P = 0.899$) (Supplementary Information, Fig. S3d), which indicates that trees were of a similar age and grew in similar conditions, based on the result of a Kruskal-Wallis test. Overall, the assumption that environmental conditions were comparable across the gradients was supported by these data. Furthermore, no significant differences across the gradient were exhibited in the measures of herbivore dung ($x_2(4) = 1.866$, $P = 0.760$) (Supplementary Information, Fig. S4a) and the percentage of holly stand bases that were browsed ($F_{(4,55)} = 1.386$, $P = 0.251$) (Supplementary Information, Fig. S4b), indicating that herbivore pressure was uniform across the dieback gradient.

There were a few other issues relating to data interpretation which should be borne in mind when interpreting the results. First, in near-natural beech forests, the mortality of overstorey trees and regeneration are typically synchronized within a period of several decades, in patches extending over several hectares[84]. The beechwoods of the New Forest differ from this situation, however, owing to the very high browsing pressure from large herbivores[24]. As a result, beech regeneration is very sparse, and dieback of woodland stands often involves conversion to non-woodland habitat, principally grassland[24]. Second, mortality processes in trees are often highly complex and difficult to interpret[85]. This complexity is illustrated by other studies of stand dieback in tree species. For example in studies of sudden dieback of aspen stands in North America, a number of different contributory and potentially interacting factors were identified, including drought, defoliation, extreme weather events and wildlife stem damage[86]. Similarly in their review of drought impacts on temperate forest stands, Bréda *et al.*[87] identify a number of different physiological mechanisms that can increase the risk of tree mortality following drought, including decreased carbon and nutrient assimilation, breakdown of the photosynthetic machinery, and reduced storage of carbohydrates. In the New Forest, causes of large beech mortality has previously been attributed to drought, with increasing frequency of droughts resulting in numerous serious water deficits since 1976, although

the evidence for this is uncertain[24]. Additional mortality factors could include significant storms that occurred in 1987 and 1990 and fungal pathogens attacks, which have been observed affecting beech the New Forest[24]. Moreover, while factors such as insect attack, frost damage and bark stripping by herbivores were not analysed here, they could have had a significant impact on mortality patterns at this site. It should also be noted that the causes of the dieback observed could also potentially be correlated with the response variables; for example, increased incidence of drought could have concurrently affected both the survival of individual trees and the ECM fungi with which they are associated.

Further, it should be noted that data were evaluated from a single sample period along a gradient of live-tree BA. Ideally, data would have been obtained by sampling the same plots before and after the initiation of tree dieback. As noted above, the only long-term data available for this study relate to one of the 12 sites surveyed, namely Denny Wood[24]. Our interpretation of the results is therefore based on the assumption that the sequential dieback of beech that has been documented at that site also applies to the other sites in the New Forest where BA gradients were surveyed. In addition, it is important to note that we interpret here differences in the ecosystem composition, structure, and function among the plots as a response to dieback. It is conceivable that the variables measured could have differed across the study area prior to the onset of dieback. For instance, soil respiration might have varied across the study area prior to the onset of dieback, and this could have contributed to some of the variation in the magnitude of dieback observed. We have no way of testing whether all of the variables measured differed between measurement locations prior to the onset of dieback, and therefore our attribution of the responses observed to dieback is based on an assumption that there was no systematic variation in these variables prior to the occurrence of dieback.

Other issues that have a bearing on the interpretation of our results include our definitions of a threshold and dieback. Here we considered a response variable to show a threshold if it met the three criteria described in the Methods. As the criteria were developed by ourselves, different results may have been obtained had other criteria been adopted. Moreover, the definition of dieback we adopted was a decline in stand BA as the central measure. This is based on the results of a review of previous research conducted by[33], into the forest ecosystem characteristics that have most often found to be significantly related to maintenance of forest biodiversity. Of these, BA is one of the forest stand structure variables most consistently associated with forest biodiversity and with aspects of the functioning of forest ecosystems, such as carbon storage[33].

Conclusion and Implications

Climate-induced forest stand dieback is rapidly increasing worldwide, in scale, magnitude, severity and speed[57]. The occurrence of thresholds in forest ecosystems undergoing dieback is a major concern, since continued environmental change may produce non-linear declines in biodiversity and ecosystem function as the result of linear changes in disturbance. Our results indicate that such thresholds can occur over a BA gradient in a forest undergoing dieback. Importantly, our results show that species richness of ECM and epiphytic lichen start to decline sharply before there is a 50% decline in BA, which implies a shift from negative feedback mechanisms to strong positive feedbacks at this threshold. In contrast, only one ecosystem function measured, namely soil respiration rate, displayed a threshold response, suggesting that biodiversity and ecosystem function threshold responses are not necessarily closely coupled. Further research is required to identify the precise mechanisms underlying the threshold responses observed, and to examine whether the observed changes are reversible.

References

1. Grimm, N. B. *et al.* The impacts of climate change on ecosystem structure and function. *Front. Ecol. Environ.* 11, 474–482, doi:10.1890/120282 (2013).

2. Rockstrom, J. *et al.* A safe operating space for humanity. *Nature* 461, 472–475, doi:10.1038/461472a (2009).

3. Steffen, W. *et al.* Planetary boundaries: Guiding human development on a changing planet. *Science* 347, doi:10.1126/science.1259855 (2015).

4. Mace, G. M. *et al.* Approaches to defining a planetary boundary for biodiversity. *Global Environ. Change* 28, 289–297, doi:10.1016/j.gloenvcha.2014.07.009 (2014).

5. Lewis, S. L. & Maslin, M. A. Defining the Anthropocene. *Nature* 519, 171–180, doi:10.1038/nature14258 (2015).

6. Huggett, A. J. The concept and utility of 'ecological thresholds' in biodiversity conservation. *Biol. Conserv.* 124, 301–310, doi:10.1016/j.biocon.2005.01.037 (2005).

7. Scheffer, M., Carpenter, S., Foley, J. A., Folke, C. & Walker, B. Catastrophic shifts in ecosystems. *Nature* 413, 591–596, doi:10.1038/35098000 (2001).

8. Keith, D. A. *et al.* Scientific foundations for an IUCN Red List of ecosystems. *PLoS ONE* 8, e62111, doi:10.1371/journal.pone.0062111 (2013).

9. Millennium Ecosystem Assessment. Millennium Ecosystem Assessment: Ecosystems and human well-being (Island Press, 2005).

10. Filotas, E. *et al.* Viewing forests through the lens of complex systems science. *Ecosphere* 5, 1–23, doi:10.1890/ES13-00182.1 (2014).

11. Anderies, J. M., Carpenter, S., Steffen, W. & Rockström, J. The topology of non-linear global carbon dynamics: From tipping points to planetary boundaries. *Environ. Res. Lett.* 8, 044048, doi:10.1088/1748-9326/8/4/044048 (2013).

12. Farley, J. & Voinov, A. Economics, socio-ecological resilience and ecosystem services. *J. Environ. Manage.* 183, 389–398, doi:10.1016/j.jenvman.2016.07.065 (2016).

13. Briske, D. D. *et al.* Catastrophic thresholds: A synthesis of concepts, perspectives, and applications. *Ecol. Soc*. 15, http://www.ecologyandsociety.org/vol15/iss3/art37 (2010).

14. Sala, O. E. & Maestre, F. T. Grass–woodland transitions: Determinants and consequences for ecosystem functioning and provisioning of services. *J. Ecol.* 102, 1357–1362, doi:10.1111/1365-2745.12326 (2014).

15. Bonan, G. B. Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science* 320, 1444–1449, doi:10.1126/science.1155121 (2008).

16. Dakos, V. *et al.* Slowing down as an early warning signal for abrupt climate change. *Proc. Nat. Acad. Sci.* 105, 14308–14312, doi:10.1073/pnas.0802430105 (2008).

17. Barnosky, A. D. *et al.* Approaching a state shift in Earth's biosphere. *Nature* 486, 52–58, doi:10.1038/nature11018 (2012).

18. Brook, B. W., Ellis, E. C., Perring, M. P., Mackay, A. W. & Blomqvist, L. Does the terrestrial biosphere have planetary tipping points? *Trends Ecol. Evol.* 28, 396–401, doi:10.1016/j.tree.2013.01.016 (2013).

19. Radford, J. Q. & Bennett, A. F. Thresholds in landscape parameters: Occurrence of the white-browed treecreeper *Climacteris affinis* in Victoria, Australia. *Biol. Conserv.* 117, 375–391, doi:10.1016/j.biocon.2003.08.002 (2004).

20. Hoegh-Guldberg, O. *et al*. Coral reefs under rapid climate change and ocean acidification. *Science* 318, 1737–1742, doi:10.1126/science.1152509 (2007).

21. Jackson, J. B. C. *et al.* Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293, 629–637, doi:10.1126/science.1059199 (2001).

22. Catalan, J. *et al*. Ecological thresholds in European alpine lakes. *Freshwater Biol.* 54, 2494–2517, doi:10.1111/j.1365-2427.2009.02286.x (2009).

23. Sasaki, T., Furukawa, T., Iwasaki, Y., Seto, M. & Mori, A. S. Perspectives for ecosystem management based on ecosystem resilience and ecological thresholds against multiple and stochastic disturbances. *Ecol. Indic.* 57, 395–408, doi:10.1016/j.ecolind.2015.05.019 (2015).

24. Martin, P. A., Newton, A. C., Cantarello, E. & Evans, P. Stand dieback and collapse in a temperate forest and its impact on forest structure and biodiversity. *For. Ecol. Manage.* 358, 130–138, doi:10.1016/j.foreco.2015.08.033 (2015).

25. Newton, A. C., Cantarello, E., Myers, G., Douglas, S. & Tejedor, N. The condition and dynamics of New Forest woodlands in *Biodiversity in the New Forest* (ed. Newton, A. C.) 132–148 (Pisces Publications, 2010).

26. Met Office. *Lyndhurst climate* http://www.metoffice.gov.uk/public/weather/climate/gcnckhuz6 (2015).

27. Tubbs, C. R. The New Forest: History, ecology and conservation (Collins, 2001).

28. Peterken, G. F. *Natural woodland: Ecology and conservation in northern temperate regions* (Cambridge University Press, 1996).

29. Newton, A. C. *Biodiversity in the New Forest* (Pisces Publications, 2010).

30. Peterken, G. F., Spencer, J. W. & Field, A. B. *Maintaining the Ancient and Ornamental woodlands of the New Forest* (Forestry Commission, 1996).

31. Flowers, N. & Tubbs, C. R. The New Forest, Hampshire: Management proposals for the un-enclosed woodlands and woodlands of special importance in the Statutory Inclosures (Nature Conservancy Council, 1982).

32. Peterken, G. F., Spencer, J. W. & Field, A. B. *Plan for the Ancient & Ornamental woodlands of the New Forest* (Forestry Commission, 1999).

33. Cantarello, E. & Newton, A. C. Identifying cost-effective indicators to assess the conservation status of forested habitats in Natura 2000 sites. *For. Ecol. Manage.* 256, 815–826, doi:10.1016/j.foreco.2008.05.031 (2008).

34. DeLuca, T., Zewdie, S., Zackrisson, O., Healey, J. & Jones, D. Bracken fern (*Pteridium aquilinum* L. Kuhn) promotes an open nitrogen cycle in heathland soils. *Plant Soil* 367, 521–534, doi:10.1007/s11104-012-1484-0 (2013).

35. Eichhorn, J. *et al*. Manual on methods and criteria for harmonized sampling, assessment, monitoring and analysis of the effects of air pollution on forests: Visual assessment of crown condition and damaging agents (UNECE ICP Forests Programme Co-ordinating Centre, 2010).

36. Jennings, S., Brown, N. & Sheil, D. Assessing forest canopies and understorey illumination: Canopy closure, canopy cover and other measures. *Forestry* 72, 59–74, doi:10.1093/forestry/72.1.59 (1999).

37. Newton, A. C. *Forest ecology and conservation: A handbook of techniques* (Cambridge University Press, 2007).

38. Jenkins, K. J. & Manly, B. A double-observer method for reducing bias in faecal pellet surveys of forest ungulates. *J. Appl. Ecol.* 45, 1339–1348, doi:10.1111/j.1365-2664.2008.01512.x (2008).

39. Bergström, R. & Guillet, C. Summer browsing by large herbivores in short-rotation willow plantations. *Biomass Bioenergy* 23, 27–32, doi:10.1016/S0961-9534(02)00027-2 (2002).

40. Gibson, D. J. *Methods in comparative plant population ecology* (Oxford University Press, 2002).

41. Reimoser, F., Armstrong, H. & Suchant, R. Measuring forest damage of ungulates: What should be considered. *For. Ecol. Manage.* 120, 47–58, doi:10.1016/S0378-1127(98)00542-8 (1999).

42. Stewart, K. E. J., Bourn, N. A. D. & Thomas, J. A. An evaluation of three quick methods commonly used to assess sward height in ecology. *J. Appl. Ecol.* **38**, 1148–1154, doi:10.1046/j.1365-2664.2001.00658.x (2001).

43. Jenkins, T. A. R. *et al*. FC woodland carbon code: Carbon assessment protocol (Forestry Commission, 2011).

44. Bates, D., Maechler, M., Bolker, B. & Walker, S. lme4: Linear mixed-effects models using Eigen and S4. *R package version* **1** (2013).

45. Wickham, H. ggplot2: Elegant graphics for data analysis. *J. Stat. Anal.* **35**, 1 (2010).

46. Nakagawa, S. & Schielzeth, H. A general and simple method for obtaining *R2* from generalized linear mixed-effects models. *Methods Ecol. Evol.* **4**, 133–142 (2013).

47. de Filho, F. J. B. O. & Metzger, J. P. Thresholds in landscape structure for three common deforestation patterns in the Brazilian Amazon. *Landsc. Ecol.* **21**, 1061–1073, doi:10.1007/s10980-006-6913-0 (2006).

48. Rocha-Santos, L. *et al*. The shrinkage of a forest: Landscape-scale deforestation leading to overall changes in local forest structure. *Biol. Conserv.* **196**, 1–9, doi:10.1016/j.biocon.2016.01.028 (2016).

49. Fahrig, L. Effect of habitat fragmentation on the extinction threshold: A synthesis. *Ecol. Appl.* **12**, 346–353, doi:10.2307/3060946 (2002).

50. Ochoa-Quintero, J. M., Gardner, T. A., Rosa, I., Barros Ferraz, S. F. & Sutherland, W. J. Thresholds of species loss in Amazonian deforestation frontier landscapes. *Conserv. Biol.* **29**, 440–451, doi:10.1111/cobi.12446 (2015).

51. Bodin, Ö., Tengö, M., Norman, A., Lundberg, J. & Elmqvist, T. The value of small size: Loss of forest patches and ecological thresholds in southern Madagascar. *Ecol. Appl.* **16**, 440–451, doi:10.1890/1051-0761(2006)016[0440:tvossl]2.0.co;2 (2006).

52. Dantas, V., Hirota, M., Oliveira, R. S. & Pausas, J. G. Disturbance maintains alternative biome states. *Ecol. Lett.* **19**, 12–19, doi:10.1111/ele.12537 (2016).

53. Dantas, V., Batalha, M. A. & Pausas, J. G. Fire drives functional thresholds on the savanna–forest transition. *Ecology* **94**, 2454–2463, doi:10.1890/12-1629.1 (2013).

54. Hoffmann, W. A. *et al*. Ecological thresholds at the savanna-forest boundary: How plant traits, resources and fire govern the distribution of tropical biomes. *Ecol. Lett.* **15**, 759–768, doi:10.1111/j.1461-0248.2012.01789.x (2012).

55. Lindner, M. *et al*. Climate change and European forests: What do we know, what are the uncertainties, and what are the implications for forest management? *J. Environ. Manage.* **146**, 69–83, doi:10.1016/j.jenvman.2014.07.030 (2014).

56. Poulter, B. *et al*. Recent trends in inner Asian forest dynamics to temperature and precipitation indicate high sensitivity to climate change. *Agric. For. Meteorol.* **178–179**, 31–45, doi:10.1016/j.agrformet.2012.12.006 (2013).

57. Allen, C. D., Breshears, D. D. & McDowell, N. G. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* **6**, 1–55, doi:10.1890/ES15-00203.1 (2015).

58. Scheffer, M. *et al*. Anticipating critical transitions. *Science* **338**, 344–348, doi:10.1126/science.1225244 (2012).

59. Muradian, R. Ecological thresholds: A survey. *Ecol. Econ.* **38**, 7–24, doi:10.1016/s0921-8009(01)00146-x (2001).

60. Scheffer, M. & Carpenter, S. R. Catastrophic regime shifts in ecosystems: Linking theory to observation. *Trends Ecol. Evol.* **18**, 648–656, doi:10.1016/j.tree.2003.09.002 (2003).

61. Lenton, T. M. & Williams, H. T. P. On the origin of planetary-scale tipping points. *Trends Ecol. Evol.* **28**, 380–382, doi:10.1016/j.tree.2013.06.001 (2013).

62. Rompré, G., Boucher, Y., Bélanger, L., Côté, S. & Robinson, W. D. Conserving biodiversity in managed forest landscapes: The use of critical thresholds for habitat. *For. Chron.* **86**, 589–596, doi:10.5558/tfc86589-5 (2010).

63. Allen, C. D. *et al*. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manage.* **259**, 660–684, doi:10.3410/f.1878956.3400064 (2010).

64. van Mantgem, P. J. *et al*. Widespread increase of tree mortality rates in the western United States. *Science* **323**, 521–524, doi:10.1126/science.1165000 (2009).

65. Walker, B. & Meyers, J. Thresholds in ecological and social–ecological systems: A developing database. *Ecol. Soc.* **9** http://www.ecologyandsociety.org/vol9/iss2/art3/ (2004).

66. Briske, D. D., Fuhlendorf, S. D. & Smeins, F. A unified framework for assessment and application of ecological thresholds. *Rangeland Ecol. Manage.* **59**, 225–236, doi:10.2458/azu_jrm_v59i3_briske (2006).

67. Corcobado, T., Moreno, G., Azul, A. M. & Solla, A. Seasonal variations of ectomycorrhizal communities in declining *Quercus ilex* forests: Interactions with topography, tree health status and *Phytophthora cinnamomi* infections. *Forestry* **88**, 257–266 (2015).

68. Teste, F. P. & Simard, S. W. Mycorrhizal networks and distance from mature trees alter patterns of competition and facilitation in dry Douglas-fir forests. *Oecologia* **158**, 193–203, doi:10.1007/s00442-008-1136-5 (2008).

69. Crowther, T. W. *et al*. Predicting the responsiveness of soil biodiversity to deforestation: A cross-biome study. *Glob. Chang. Biol.* **20**, 2983–2994, doi:10.1111/gcb.12565 (2014).

70. de Vries, F. T. *et al*. Soil food web properties explain ecosystem services across European land use systems. *Proc. Natl. Acad. Sci. USA* **110**, 14296–14301, doi:10.1073/pnas.1305198110 (2013).

71. Ehrenfeld, J. G., Ravit, B. & Elgersma, K. Feedback in the plant-soil system. *Annu. Rev. Envir. Res.* **30**, 75–115, doi:10.1146/annurev.energy.30.050504.144212 (2005).

72. Simard, S. W. *et al*. Mycorrhizal networks: Mechanisms, ecology and modelling. *Fungal Biol. Reviews* **26**, 39–60, doi:10.1016/j.fbr.2012.01.001 (2012).

73. Sillett, S. C., McCune, B., Peck, J. E., Rambo, T. R. & Ruchty, A. Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. *Ecol. Appl.* **10**, 789–799, doi:10.1890/1051-0761(2000)010[0789:DLOELR]2.0.CO;2 (2000).

74. Paltto, H., Nordberg, A., Nordén, B. & Snäll, T. Development of secondary woodland in oak wood pastures reduces the richness of rare epiphytic lichens. *PLoS ONE* **6**, e24675, doi:10.1371/journal.pone.0024675 (2011).

75. Hibbard, K. A., Law, B. E., Reichstein, M. & Sulzman, J. An analysis of soil respiration across northern hemisphere temperate ecosystems. *Biogeochemistry* **73**, 29–70, doi:10.1007/s10533-004-2946-0 (2005).

76. Ryan, G. M. & Law, E. B. Interpreting, measuring, and modeling soil respiration. *Biogeochemistry* **73**, 3–27, doi:10.1007/s10533-004-5167-7 (2005).

77. Holden, S. R. & Treseder, K. K. A meta-analysis of soil microbial biomass responses to forest disturbances. *Front. Microbiol*. **4**, doi:10.3389/fmicb.2013.00163 (2013).

78. Martin, P., Newton, A. C., Cantarello, E. & Evans, P. M. Analysis of ecological thresholds in a temperate forest undergoing dieback (in press).

79. Fukami, T. & Wardle, D. A. Long-term ecological dynamics: Reciprocal insights from natural and anthropogenic gradients. *Proc. R. Soc. Lond. [Biol.]* **272**, 2105–2115, doi:10.1098/rspb.2005.3277 (2005).

80. Geßler, A. *et al*. Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. *Trees* **21**, 1–11 (2007).

81. Packham, J. R., Thomas, P. A., Atkinson, M. D. & Degen, T. Biological flora of the British Isles: *Fagus sylvatica*. *J. Ecol.* **100**, 1557–1608, doi:10.1111/j.1365-2745.2012.02017.x (2012).

82. Natural England and RSPB. *Climate change adaptation manual: Evidence to support nature conservation in a changing climate* (Natural England and RSPB, 2014).

83. Cavin, L., Mountford, E. P., Peterken, G. F. & Jump, A. S. Extreme drought alters competitive dominance within and between tree species in a mixed forest stand. *Funct. Ecol.* **27**, 1424–1435, doi:10.1111/1365-2435.12126 (2013).

84. Newton, A. C., Cantarello, E., Tejedor, N. & Myers, G. Dynamics and conservation management of a wooded landscape under high herbivore pressure. *Int. J. Biodivers.* **2013**, 15, doi:10.1155/2013/273948 (2013).

85. Franklin, J. F., Shugart, H. H. & Harmon, M. E. Tree death as an ecological process. *BioScience* **37**, 550–556, doi:10.2307/1310665 (1987).

86. Frey, B. R., Lieffers, V. J., Hogg, E. H. & Landhäusser, S. M. Predicting landscape patterns of aspen dieback: Mechanisms and knowledge gaps. *Can. J. For. Res.* **34**, 1379–1390, doi:10.1139/x04-062 (2004).

87. Bréda, N., Huc, R., Granier, A. & Dreyer, E. Temperate forest trees and stands under severe drought: A review of ecophysiological responses, adaptation processes and long-term consequences. *Ann. For. Sci.* **63**, 625–644, doi:10.1051/forest:2006042 (2006).

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Author Contributions

Conceived and designed study: A.N., P.M.E., E.C. Collected the majority of field data: P.M.E., E.C., N.S., A.N., L.F. Performed laboratory experiments: P.M.E., E.C. Analysed non-arthropod data: P.M.E, P.M. Collected arthropod data, carried out DNA barcoding and wrote arthropod methods: N.B., J.E.C., S.W.A. Wrote the paper: P.M.E., A.N. All authors gave final approval for publication.

Additional Information

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Appendix 2.6: Supplementary Information for 'Thresholds of biodiversity and ecosystem function in a forest ecosystem undergoing dieback', the published version of Chapter 2

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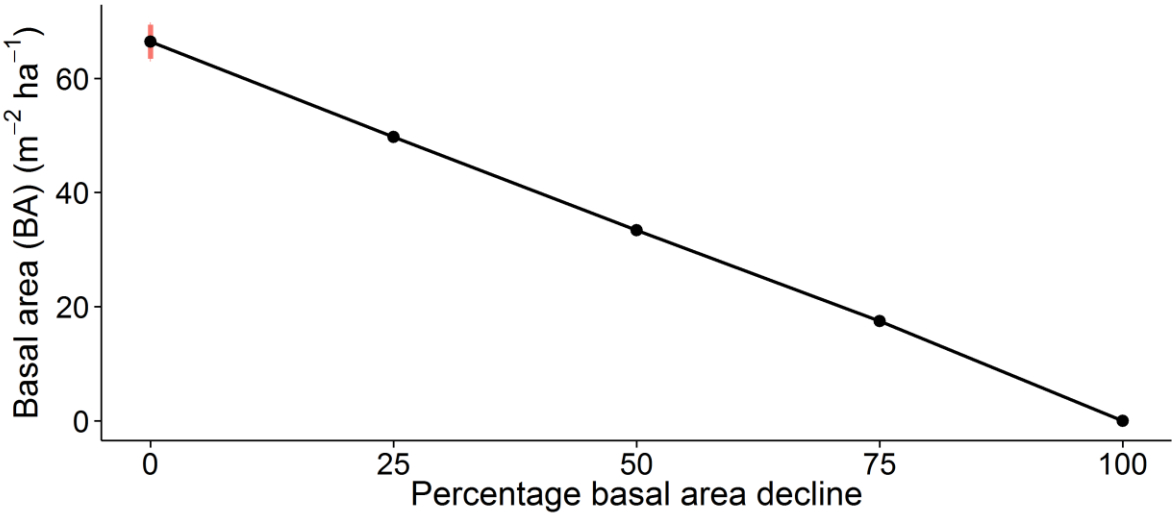
Inventory of Supplementary Information:

Fig. S1: The mean stand basal area (BA) of dieback stages of the gradient plots. Standard error bars are



shown in red.

Table S1: Basal area (BA) statistics. Mean, standard deviation (SD), standard error (SE), confidence interval (CI), minimum (Min) size of BA and maximum (Max) size of BA for each of the stages of dieback.

		BA					
Percent basal area decline	**N**	**Mean**	**SD**	**SE**	**CI**	**Min**	**Max**
0%	12	66.42	10.29	2.97	6.54	59.85	98.39
25%	12	49.71	1.36	0.39	0.86	47.73	52.12
50%	12	33.37	1.79	0.52	1.14	30.58	37.12
75%	12	17.45	1.47	0.42	0.93	13.65	19.44
100%	12	0	0	0	0	0	0

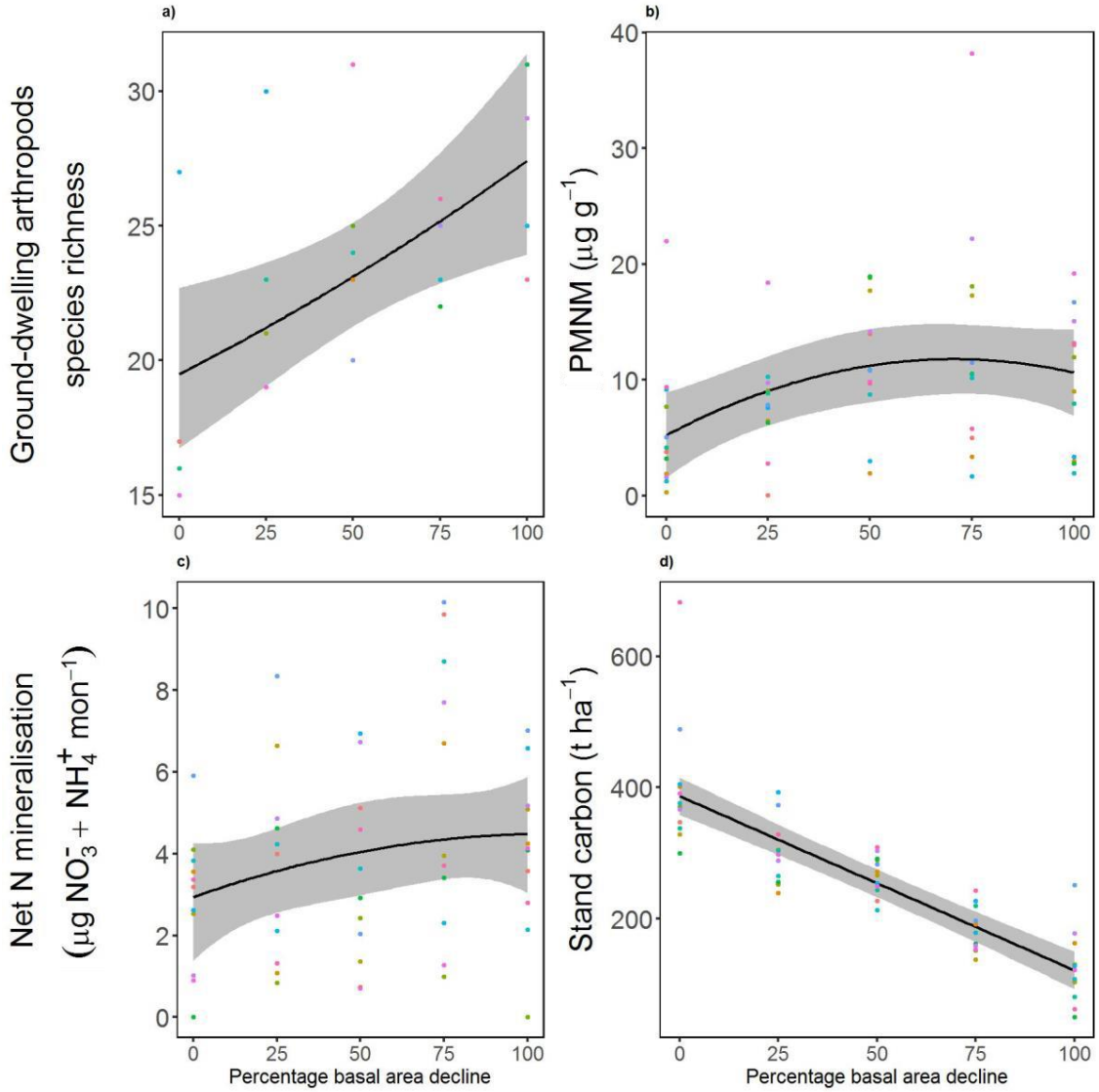


Fig. S2: Non-threshold relationships between stage of dieback and ecosystem processes. Relationships between stage of dieback and a) ground-dwelling arthropods (n = 25); b) potentially mineralisable nitrogen in the mineral layer (PMNM) (n = 60); c) net mineralisation per month (n = 55); and d) total stand carbon (n = 60). The black lines represent prediction using the most parsimonious model coefficients and grey shading the 95% confidence intervals of the coefficients (marginal r^2 =0.26, 0.07, 0.13, and 0.50 for a-d, respectively). Net mineralisation was measured as the amount of NH_4^+ and NO_3^- taken up by a resin capsule over a four-month period and then divided by 4 to obtain a value per month. The different coloured points represent the values at each individual site.

Supplementary Methods: SM1

Plot set-up

Each plot was 20 x 20 m (400 m^2; 0.04 ha). The edges were delineated with measuring tapes. A compass was used to confirm that the adjacent angles were at 90˚ angles. A nested sub-plot of 10 x 10 m (100 m^2) was set up in the centre of each plot, laid out in the same orientation as the full plot. The centre and the corners of the sub-plot were marked with wooden stakes for easy identification on return visits. The mid-points of each plot were recorded using a handheld GPS (GPSMAP 60CSx; Garmin, USA).

Structural survey

The diameters at breast height (dbh) of both living and dead standing trees (snags) were measured at 1.3 m using a diameter tape pulled taut horizontally to the trunk. Following advice and procedures from Husch *et al.*[1] and van Laar and Akça[2], specific instructions were followed when using diameter tapes for difficult trees. The combined dbhs were used to calculate the overall BA [3], forming the basis of the primary criterion.

Crown condition

Living beech trees were further assessed for their condition, undertaken using binoculars at several points around each tree where visibility was good. The condition attributes were the potential crown loss, live growth loss, condition of the current branches and discolouration of the crown. Potential crown loss and leave loss were recorded as a percentage based on the average values provided by two observers. Similarly, condition was recorded as number (1-4) based on the descriptions. Any pathogens present were also recorded after a thorough search of the lower sections of each tree.

Canopy openness

At each corner of the 10 x 10 m sub-plot four readings were taken using a spherical densiometer, one in each cardinal direction, giving an overall average for that plot[4].

Understorey openness

Understorey openness was determined the same way as canopy openness, but only for trees less than approximately 6 m in height.

Forest biomass

Following Jenkins *et al.*[5], oven-dry biomass was determined in four different components of the stand; the roots, the tree stems, the branches and foliage. To calculate the total biomass of a single species, the stem biomass, crown biomass and root biomass were summed together and multiplied by the number of that species present in the plot. The total biomass of all species was then calculated by summating all individual species' biomass values. The oven-dry biomass was calculated based on specific values for broadleaves, taken from McKay *et al*[6].

Carbon assessment for trees

Carbon content of a plot was calculated by multiplying the oven-dry matter biomass by 0.5, the carbon fraction of biomass[7].

Herbivore pressure metrics

To account for the relative presence and influence of herbivores, understorey crown condition, browseline, sward height, seedling and sapling abundance, browsing intensity, dung counts, and presence of a shrub layer were recorded.

For living trees in the understorey, crown condition (average of two different observers) was recorded based on deviation from perceived 'pristine' condition (i.e. 100%). Percentage of discolouration, percentage of leaves remaining, potential crown structure, empty branches and position of the tree were taken into account.

The browse lines of palatable (e.g. beech, oak, birch) and unpalatable (e.g. holly, hawthorn) trees were recorded if they were within the edges of the plot. Using a marked range pole, any branches that were higher than 1.8 m (a deer's maximum browse height), but lower than 2.3 m (based on an average drop of 50 cm in the winter), were counted as browsed. Any branches that retained leaves below 1.8 m were counted as unbrowsed. A percentage ratio of browsed to unbrowsed was calculated. The sward height was measured using a measuring stick, based on the findings of Stewart *et al.*[8] This was measured in the centre and at the four corners of the sub-plot, and a mean value was recorded.

The percentages cover of mosses, bare ground, bracken, trampling and ground flora were recorded from a detailed visual assessment of each plot. Similarly, seedling (< 1.3 m in

height) and sapling (> 1.3 m and dbh < 10 cm) abundances were assessed through a manual search of the entire 20 x 20 m plot. Seedlings were any counted if they were older than a year, based on physical aspects.

Partial defoliation or complete consumption of plants occur through herbivore browsing, the intensity of which is commonly determined by counts of un-browsed and browsed branches[9,10]. This was undertaken using a random stratified design. Initially, a 2 x 2 m quadrat was placed in the most south-westerly corner of the sub-plot, continuing clockwise (NW, NE, SE) around the corners, until 100 stems had been assessed. The same technique was used for assessing bramble browsing, following Bazely *et al* [11].

For estimating herbivore abundance from dung, the faecal standing crop (FSC) method, the most commonly used and efficient technique[12,13], was used. A manual dung count was carried out in the sub-plot; the amount, condition and the species recorded. Following Jenkins and Manly[14], the individual pellets/ bolus and their condition were recorded. The faecal matter of different animals (deer, *Equus* species, rabbits and cattle) were recorded separately.

Soil survey

Following the methods of DeLuca *et al.*[15], ten separate soil samples were taken in randomly-stratified positions, two from the centre and two at each corner of the nested 10 x 10 m sub-plot, for both the O horizon and A horizon soil layer (0-15 cm below the O horizon). The vegetation the sample was taken under (e.g. bracken, grass) was noted.

For bulk density (BD) measurements, three 100 cm^3 stainless steel rings were inserted into the soil to ensure a known volume. These were taken from the SW and NE corners and from the mid-point.

For analyses of NO_3^- and NH_4^+, 5 g of sieved, field-moist soil was placed into a labelled tube with 25 ml of 1 M KCl added. The soils were shaken by hand and placed horizontally on a rotary shaker for 30 minutes at 250 rev/min. The extracts were immediately filtered through a Fisher QT 210 filter paper into a labelled polypropylene vial. The filtrates were then frozen immediately and analysed two months later. Both NH_4^+ and NO_3^- were analysed using the microplate-colorimetric technique, with the salicylate-nitroprusside method for NH_4^+, following Mulvaney[16] and the vanadium method for NO_3^-[17].

To determine the potential mineralisable nitrogen concentrations, 5 g of sieved, field-moist soil was placed into a labelled tube with 25 ml of ultrapure water added. The headspace was then flushed with N_2 (g). The tube was sealed and incubated for 7 days at 40°C [18]. Immediately after incubation, 1.75 g of KCl was added to each tube. The tubes were shaken (1 hr at 200 rev/min), centrifuged and filtered immediately, using the process as for NO_3^- and NH_4^+. The pH and electrical conductivity of soil was determined using a 2:1 deionized water to soil ratio.

Net N mineralisation and nitrification:

To enable analysis of in-situ of nitrification and N mineralisation rates, following DeLuca *et al.*[15], a polyester mesh ionic resin capsule (Unibest, Walla Walla, WA, USA) was buried in the centre of each plot, 10 cm deep into the mineral layer. The capsules were placed between 9th October and 12th November, 2014 and were removed from the ground four months later.

The nitrogen mineralisation and nitrification of a plot were analysed through leaching of resin capsules (RC). Initially, 10 mL of 1 M KCl was placed into each tube containing a RC, which was then shaken horizontally for 30 minutes at 250 rpm. The extractant was poured into a clean storage tube. This process was repeated two more times, making a total of 30 mL of the extractant. The extractant was centrifuged at 4000 rpm for 10 minutes. 20 mL of the supernatant was then pipetted into a 30 mL polypropylene tube and frozen prior to colorimetric analysis as described above.

Soil respiration rate:

Soil respiration rate was measured using a SR-1 closed chamber Infra-red gas analyser (PP Systems, Amesbury, MA, USA). All measurements were recorded between 10:00 and 14:00 on sunny days within a month of each other. After automatic flushing and calibration of the chamber, the PVC chamber was inserted 2 cm into the soil after any vegetation had been removed from the surface. The CO_2 concentration was measured continuously for 2 minutes. Five measurements were taken from each survey plot and then averaged to produce a mean soil respiration rate for the whole plot. Soil respiration rate was calculated as in (PP Systems[19]:

$$R=V/A \times ((Cn-Co)/(Tn))$$

Where *R* is the respiration rate, *V* is the volume of the chamber, *A* is the area of soil exposed, *Cn* is the CO_2 concentration at time 0, and *Co* is the CO2 concentration at time, *Tn* (120 seconds in this study).

Soil moisture

Soil moisture was measured as the difference in weight of a 5 g moist soil sample before and after oven-drying. Sieved mineral and organic samples were oven-dried at 105 °C and 80 °C, respectively, until they remained a constant weight. To measure the soil organic matter (SOM), the oven-dried samples were then placed in a 500 °C furnace overnight (12 hours), the final weight recorded after being cooled in a desiccator. LOI = 100 x (mass of oven-dry soil-mass of ignited soil)/ mass of oven-dry soil = g per 100g oven-dry soil[20]. The soil was dried at 105 °C for 24 h and then sieved (2 mm) to remove stones and other non-soil material (>2 mm diameter). Bulk density was calculated by dividing soil mass (less stone mass) by core volume (less stone volume).

Soil content and structure

The Forest Research (FR) team at Alice Holt Lodge, Surrey, measured the exchangeable cations/anions of K, S, Ca, Mg, Na, Al, Mn and F; total N and C, organic and inorganic C; the plant-available P; and the particle sizes of the soil from air-dried samples. Following FR methods, the exchangeable cations/anions were analysed using $BaCl_2$ extraction (FR Reference method: ISO 11260 & 14254). First, a soil suspension of 3 g soil and 36 ml of 0.1 M $BaCl_2$ was shaken for 60 minutes, centrifuged and filtered with 0.45 µm syringe filter. Extracts were then acidified and analysed using a dual view ICP-OES (Thermo ICap 6500 duo). The Olsen P method with ADAS index was used to determine the amount of phosphorus available (FR Reference method: The analysis of Agricultural Materials MAFF 3rd Edition RB427). A suspension of 5 g soil with 100 ml of sodium bicarbonate solution was buffered at pH 8.5. The solution was shaken for 30 min on an orbital shaker, centrifuged and filtered with 0.45µm syringe filters. Extracts were then acidified with 1.5 M sulphuric acid and mixed with a solution of ascorbic acid and ammonium molybdate for 10 min and then measured at 880 nm with a Shimadzu UV sprectrophotometer. Total C and N were analysed using a Carlo Erba CN analyser (Flash1112 series) and combustion method (FR Reference method: ISO 10694 & 13878). Samples were ball-milled for homogenisation and then around 30 mg weighed in tin capsules, pressed and measured using the analyser. Following, 30 g of soil was placed in

a silver capsule to quantify inorganic C. The silver capsule was put furnace at 500^{o}C for 2 hours, which removed the organic carbon. The organic carbon fraction was calculated as the difference between total carbon and inorganic carbon. The soil particle size distribution was determined using a Laser Diffraction Particle Sizer (FR Reference method: Laser diffraction); 30 g of soil were suspended in water and passed through the flow cell of the analyser (Beckman Coulter LS13320).

Data analysis

Random intercepts and slopes were included for each site. All the variables were tested for normal distribution with the Shapiro–Wilk test and for homogeneity of variances for Bartlett's test[21]. Data that did not fit these assumptions were log-transformed prior to analysis.

Count data were modelled using a Poisson error structure. For proportional and percentage data, a small non-zero value was added to avoid infinite logit transformed values[22]. AICc values were calculated using the maximum likelihood value of the model[23]. AICc values were determined using the MuMIn R package[24] and used to define the most parsimonious model, following an information theoretic approach[23]. Performance of models was evaluated by calculating the marginal r^{2} [25].

Supplementary Methods: SM2

Ground-dwelling arthropods collection

Pitfall trapping was carried out in five out of the 12 sites. In each site eight pitfall traps were placed on the perimeter of the 10m x 10m sub-plot; one in each corner and one midway along each edge. A soil auger was used to create holes in which plastic cups (8 cm in diameter and 11 cm tall) were placed. Approximately 3 cm of propylene glycol, a cost effective preservative, was poured into each cup. Water was allowed to escape through the use of drainage holes in the top of the cups; this also prevented the trap flooding. A galvanised steel square which was supported by turned-down corners was placed over each trap. Forestry Commission staff collected the contents of each pitfall trap weekly from late May to late July 2014, totalling eight collections and 56 trapping days. The arthropod material from the eight pitfall traps in each plot were pooled into a single labelled and sterilised 1 litre sample bottle and then stored in -5 °C to preserve the specimens for metabarcoding.

Ground-dwelling arthropods analysis

DNA metabarcoding was employed for invertebrate identification using a methodology tailored from the approach described in Yu *et al.*[26]. Samples were stored in absolute ethanol at 4°C, followed by the extraction of DNA using the Qiagen blood and tissue extraction kit. Polymerase Chain Reactions (PCR) were performed targeting the 658 base pair C terminal region in the gene encoding the mitochondrial cytochrome oxidase subunit I (COI); primers used for the COI region of interest were: Forward: LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and Reverse: mlCOIintGLR (5'-GGNGGR TANANNGTYCANCCNGYNCC-3'). Three separate PCRs were carried out for each sample. An aliquot was checked on a 1.4% agarose gel and then the PCRs pooled before library construction. A multiplex identifier (MID) tag was attached to the forward primer in addition to the relevant adaptor for the sequencing platform. The MID tag was specific to each sample and allowed multiple samples to be pooled for sequencing and then separated out bioinformatically afterwards. A touch-down thermocycling profile was used, followed by a low number of cycles with an intermediate annealing temperature. Indexing barcodes were added to the amplicons following the Illumina TruSeq Nano protocol from the 'Clean-up Fragmented DNA' stage. In a deviation from this protocol fragments were size-selected using blue Pippin size selection of the 300-670bp region to remove larger fragments. The barcoded samples were pooled into a single pool and 250bp paired end reads were generated on one lane of the Illumina MiSeq platform. The pool

was demultiplexed into the individual samples using the Illumina bcl2fastq (v 1.8.4bin) software. The samples were clustered into OTUs (operational taxonomic units) using the approach described in Yu *et al.*[27] starting with demultiplexed samples in step 1. Instead of the described step 6 of the pipeline we used the BOLD database and website for taxonomic assignment and confidence assessment. Accepted matches had to have at least 97% sequence similarity at a given taxonomic level. For this we queried the website by using a custom script that created the urls and parsed the output for each OTU. In a final step the taxonomic assignment, OTU and the number of reads of each sample mapping to the OTUs was collated into a single table. The final species lists were checked against previous records of species occurrence in Britain using primarily the National Biodiversity Networks Gateway[27] but also Fauna Europaea[28], Antweb[29], the British Arachnological Society[30,] and Araneae: Spiders of Europe[31]. Where no previous record was found to species level, occurrence in Britain to Genus level was checked.

Table S2: Summary of variables measured and units used.

Variable	Biodiversity (B), ecosystem function (EF) or ecosystem condition (EC) measure?	Units
Ectomycorrhizal fungi species richness	B	Unique species 0.04 ha^{-1}
Sward height	EC	Cm
Abundance of holly seedlings	EC	Individuals 0.04 ha^{-1}
Abundance of beech seedlings	EC	Individuals 0.04 ha^{-1}
Abundance of oak seedlings	EC	Individuals 0.04 ha^{-1}
Abundance of tree seedlings	EC	Individuals 0.04 ha^{-1}
Abundance of palatable seedlings	EC	Individuals 0.04 ha^{-1}
Bulk density of the soil	EC	g cm^{-3}
Depth of the organic layer	EC	Cm
Average diameter at breast height of beech trees	EC	cm
Average height of beech trees	EC	m
Volume of standing deadwood in a plot	EC	m^3 ha^{-1}
Volume of lying deadwood in a plot	EC	m^3 ha^{-1}
C/N ratio of the soil	EF	C/N ratio
Potassium exchangeable cations concentration in the mineral layer soil	EF	cmol(+)/kg
Magnesium exchangeable cations concentration in the mineral layer soil	EF	cmol(+)/kg
Sodium exchangeable cations concentration in the mineral layer soil	EF	cmol(+)/kg
Calcium exchangeable cations concentration in the mineral layer soil	EF	cmol(+)/kg

Manganese exchangeable cations concentration in the mineral layer soil	EF	cmol(+)/kg
Iron exchangeable cations concentration in the mineral layer soil	EF	cmol(+)/kg
Aluminium exchangeable cations concentration in the mineral layer soil	EF	cmol(+)/kg
Availability of soil phosphorus	EF	mg kg^{-1}
Total soil nitrogen	EF	% of soil
Total soil carbon	EF	% of soil
Soil pH	EF	pH
Electrical conductivity	EF	mS m^{-1}
Net ammonification	EF	µg NH_4^+ $capsule^{-1}$ mon^{-1}
Net nitrification	EF	µg NO_3^- $capsule^{-1}$ mon^{-1}
Net mineralisation	EF	µg NH_4^+ and NO_3^- $capsule^{-1}$ mon^{-1}
Soil respiration rate	EF	µmol m^{-2} s^{-1}
Soil temperature	EF	°C
Total stand carbon (vegetation, deadwood and soil)	EF	t ha^{-1}
Aboveground biomass	EC	t ha^{-1}
Soil clay percentage	EC	% 0-2 µm soil particles
Soil silt percentage	EC	% 2-63 µm soil particles
Soil sand percentage	EC	% 63 µm-2 mm soil particles
Bracken cover	EC	% cover 0.04 ha^{-1}
Bare ground and moss cover	EC	% cover 0.04 ha^{-1}
Litter cover	EC	% cover 0.04 ha^{-1}
Grass cover	EC	% cover 0.04 ha^{-1}
Palatable tree browseline	EC	% browseline (above 1.8 m) 0.04 ha^{-1}

Unpalatable tree browseline	EC	% browseline (above 1.8 m) 0.04 ha^{-1}
Holly cover	EC	% cover 0.04 ha^{-1}
Rubus cover	EC	% cover 0.04 ha^{-1}
Holly shrubs browsed	EC	% browse of available plants
Rubus shrubs browsed	EC	% browse of available plants
Average crown condition	EC	% condition
Understorey condition	EC	% condition
Canopy openness	EC	% sky visible
Understorey openness	EC	% sky visible
Tree seedling richness	B	Unique species 0.04 ha^{-1}
Tree sapling richness	B	Unique species 0.04 ha^{-1}
Spider species richness	B	Unique species 0.04 ha^{-1}
Rove beetles species richness	B	Unique species 0.04 ha^{-1}
Carabid beetles species richness	B	Unique species 0.04 ha^{-1}
Ant species richness	B	Unique species 0.04 ha^{-1}
Weevil species richness	B	Unique species 0.04 ha^{-1}
Woodlice species richness	B	Unique species 0.04 ha^{-1}
Ground-dwelling arthropod species richness	B	Unique species 0.04 ha^{-1}
Moisture content of the mineral layer	EF	% soil moisture
Moisture content of the organic layer	EF	% soil moisture
Cervus dung proportional	EC	see Jenkins and Manly (2008)

Equus dung proportional	EC	see Jenkins and Manly (2008)
Proportional dung total	EC	see Jenkins and Manly (2008)
Very large beech trees (74.97 cm < dbh < 103 cm)	EC	Individuals 0.04 ha^{-1}
Large beech trees (68.32 cm < dbh < 74.97 cm)	EC	Individuals 0.04 ha^{-1}
Holly tree abundance	EC	Individuals 0.04 ha^{-1}
Beech trees abundance	EC	Individuals 0.04 ha^{-1}
Holly saplings abundance	EC	Individuals 0.04 ha^{-1}
Beech saplings abundance	EC	Individuals 0.04 ha^{-1}
Overall saplings abundance	EC	Individuals 0.04 ha^{-1}
Ground flora species richness	B	Unique species 0.04 ha^{-1}
Woody ground flora species richness	B	Unique species 0.04 ha^{-1}
Non-woody ground flora species richness	B	Unique species 0.04 ha^{-1}
Lichen species richness	B	Unique species 0.04 ha^{-1}
Lichen species richness on holly	B	Unique species 0.04 ha^{-1}
Lichen species richness on beech	B	Unique species 0.04 ha^{-1}
Organic layer loss on ignition	EC	% weight loss
Mineral layer loss on ignition	EC	% weight loss
Organic layer nitrate concentration	EF	$mg\ kg^{-1}$
Mineral layer nitrate concentration	EF	$mg\ kg^{-1}$
Organic layer ammonium concentration	EF	$mg\ kg^{-1}$
Mineral layer ammonium concentration	EF	$mg\ kg^{-1}$
Potentially mineralisable nitrogen of the organic layer	EF	$\mu g\ g^{-1}$

Potentially mineralisable nitrogen of the mineral layer	EF	μg g^{-1}
Understorey biomass	EC	t ha^{-1}

Table S3: Generalised linear mixed models used to determine whether a threshold was exhibited in all the response variables and associated measures of parsimony (AICc), support (ΔAICc, AICc) and goodness of fit (Marginal r^2). Model strucutre that contained a BA decline + BA decline^2 terms indicated a non-linear response; model strucutre that contained a BA decline term indicated a linear response; and Null model specifies that the model indicated little or no change over the gradient of BA loss. The degrees of freedom for each model was the number of terms in the model structure plus two.

Response variable	Model structure	Log likelihood	AICc	ΔAICc	Marginal r^2	Threshold?
Ectomycorrhizal fungi species richness	BA decline + BA decline^2	-149.4	307.526	0	0.568	Yes
	BA decline	-154.7	315.824	8.298	0.463	
	Null model	-185.13	374.476	66.949	0	
Sward height	BA decline + BA decline^2	-264.5	540.106	0	0.507	Yes
	BA decline	-274.56	557.849	17.743	0.416	
	Null model	-294.11	594.648	54.542	0	
Abundance of holly seedlings	BA decline + BA decline^2 +log(Dung)	-1332.8	2676.8	0	0.119	No
	BA decline +log(Dung)	-1844.6	3697.83	1021.03	0.047	
	Null model	-1891.8	3790.04	1113.25	0.007	
Abundance of beech seedlings	BA decline + BA decline^2 + log(Dung)	-275.66	562.439	0	0.216	Yes
	BA decline + log(Dung)	-297.96	604.637	42.198	0.169	
	Null model	-331.09	668.61	106.172	0.015	
Abundance of oak seedlings	BA decline+ BA decline^2	-50.194	111.499	0	0.455	Yes

	+ log(Dung)					
	BA decline + log(Dung)	-57.726	124.178	12.679	0.176	
	Null model	-62.773	131.974	20.474	0.035	
Abundance of tree seedlings	BA decline+ BA decline^2 + log(Dung)	-1372.8	2756.79	0	0.134	No
	BA decline + log(Dung)	-1902.9	3814.57	1057.78	0.051	
	Null model	-1967.1	3940.64	1183.85	0.001	
Abundance of palatable seedlings	BA decline + BA decline^2 + log(Dung)	-265.39	541.9	0	0.294	Yes
	BA decline + log(Dung)	-294.34	597.407	55.507	0.226	
	Null model	-332.49	671.411	129.511	0.004	
Bulk density of the soil	Null model	17.94	-29.452	0	0	No
	BA decline	17.35	-25.973	3.479	0.033	
	BA decline + BA decline^2	16.84	-22.568	6.883	0.038	
Depth of the organic layer	Null model	-26.75	59.929	0	0	No
	BA decline	-27.262	63.251	3.322	0.016	
	BA decline + BA decline^2	-26.234	63.58	3.651	0.038	
Average diameter at breast height of beech trees	BA decline + BA decline^2	-182.94	377.303	0	0.007	No
	BA decline	-187.3	383.531	6.228	0.003	
	Null model	-190.1	386.737	9.434	0	

Average height of beech trees	BA decline + BA decline^2	-150.09	311.599	0	0.046	No
	BA decline	-153.72	316.376	4.777	0.044	
	Null model	-157.01	320.567	8.968	0	
Volume of standing deadwood in a plot	BA decline + BA decline^2	-606.23	1223.58	0	0.043	No
	BA decline	-616.5	1241.73	18.148	0.042	
	Null model	-627	1260.42	36.843	0	
Volume of lying deadwood in a plot	BA decline + BA decline^2	-74.148	159.407	0	0.448	No
	BA decline	-75.534	159.796	0.388	0.443	
	Null model	-93.483	193.394	33.987	0	
C/N ratio of the soil	BA decline + BA decline^2 + pH	-154.33	319.77	0	0.06	No
	BA decline + pH	-156.8	322.325	2.555	0.056	
	Null model	-161.11	328.647	8.877	0	
Potassium exchangeable cations concentration in the mineral layer soil	Null model	76.59	-146.75	0	0.199	No
	BA decline + pH	77.626	-146.53	0.225	0.317	
	BA decline + BA decline^2 + pH	76.036	-140.96	5.791	0.316	
Magnesium exchangeable cations concentration in the mineral layer soil	BA decline + BA decline^2 + pH	-105.07	223.724	0	0.035	No
	BA decline + pH	-106.55	224.22	0.495	0.035	
	Null model	-111.6	229.631	5.907	0	

Sodium exchangeable cations concentration in the mineral layer soil	BA decline + pH	110.275	-209.44	0	0.335	No
	BA decline + BA decline^2 + pH	107.98	-202.38	7.063	0.332	
	Null model	102.076	-197.72	11.715	0	
Calcium exchangeable cations concentration in the mineral layer soil	BA decline + pH	17.362	-23.612	0	0.175	No
	BA decline + BA decline^2 + pH	16.642	-19.699	3.914	0.173	
	Null model	11.842	-17.256	6.356	0	
Manganese exchangeable cations concentration in the mineral layer soil	Null model	88.883	-171.34	0	0.065	No
	BA decline + pH	85.913	-163.1	8.238	0.065	
	BA decline + BA decline^2 + pH	84.722	-158.33	13.006	0.085	
Iron exchangeable cations concentration in the mineral layer soil	BA decline + BA decline^2 + pH	-268.34	547.793	0	0.085	No
	BA decline + pH	-273.18	555.087	7.294	0.072	
	Null model	-279.19	564.801	17.008	0	
Aluminium exchangeable cations concentration in the mineral layer soil	Null model	-38.524	83.476	0	0	No
	BA decline + pH	-37.721	84.169	0.693	0.031	
	BA decline + BA decline^2 + pH	-37.576	86.262	2.786	0.031	
Availability of soil phosphorus	Null model	72.697	-138.97	0	0	No
	BA decline	69.793	-130.86	8.108	0	

	+ pH					
	BA decline + BA decline^2 + pH	68.117	-125.12	13.844	0	
Total soil nitrogen	Null model	-61.364	129.156	0	0	No
	BA decline + pH	-62.091	135.293	6.137	0.007	
	BA decline + BA decline^2 + pH	-61.363	136.312	7.156	0.009	
Total soil carbon	BA decline + BA decline^2 + pH	-228.01	469.603	0	0.076	No
	BA decline + pH	-232.05	475.208	5.605	0.068	
	Null model	-240.08	486.589	16.986	0	
Soil pH	Null model	-16.753	39.934	0	0	No
	BA decline + BA decline^2	-16.862	44.835	4.901	0.037	
	BA decline	-18.058	44.844	4.909	0	
Electrical conductivity	Null model	219.607	-432.79	0	0.105	No
	BA decline	215.273	-421.82	10.966	0.136	
	BA decline + BA decline^2	213.517	-415.92	16.863	0.213	
Net ammonification	Null model	-88.247	182.964	0	0.047	No
	BA decline + BA decline^2	-86.432	184.088	1.125	0.052	
	BA decline	-87.779	184.358	1.394	0.057	
Net nitrification	BA decline + BA decline^2	-90.104	191.433	0	0.104	No

	BA decline	-91.485	191.77	0.337	0.103	
	Null model	-95.775	198.02	6.587	0	
Net mineralisation	BA decline + BA decline^2 + pH	-118.42	250.589	0	0.069	No
	BA decline + pH	-120.62	252.466	1.877	0.064	
	BA decline + BA decline^2	-120.97	253.168	2.579	0.065	
	BA decline	-123.25	255.303	4.715	0.056	
	Null model	-125.97	258.414	7.825	0	
Soil respiration rate	BA decline + BA decline^2	-80.996	173.1	0	0.155	Yes
	BA decline	-84.043	176.8	3.71	0.103	
	Null model	-87.376	181.2	8.08	0	
Soil temperature	BA decline + BA decline^2	-99.623	210.356	0	0.136	No
	BA decline	-101.86	212.443	2.087	0.122	
	Null model	-108.71	223.845	13.488	0	
Total stand carbon (vegetation, deadwood and soil)	BA decline	266.419	-524.11	0	0.501	No
	BA decline + BA decline^2	267.038	-522.97	1.145	0.584	
	Null model	251.796	-497.16	26.946	0	
Aboveground biomass	BA decline	-340.95	690.621	8.496	0.537	No
	BA decline + BA decline^2	-335.51	682.124	0	0.534	
	Null model	-372.15	750.723	68.599	0	
Soil clay percentage	Null model	-16.773	39.975	0	0	No
	BA decline	-18.002	44.73	4.756	0.003	

	BA decline + BA decline^2	-18.164	47.439	7.465	0.004	
Soil silt percentage	Null model	2.618	1.193	0	0	No
	BA decline	2.658	3.411	2.218	0.043	
	BA decline + BA decline^2	2.195	6.721	5.528	0.043	
Soil sand percentage	Null model	-20.488	47.404	0	0	No
	BA decline	-21.116	50.958	3.554	0.014	
	BA decline + BA decline^2	-21.213	53.536	6.133	0.014	
Bracken cover	BA decline + BA decline^2	-137.02	285.155	0	0.245	No
	BA decline	-139.11	286.952	1.797	0.245	
	Null model	-150.3	307.035	21.88	0	
Bare ground and moss cover	BA decline + BA decline^2	-101.16	213.425	0	0.199	No
	BA decline	-103.56	215.847	2.422	0.175	
	Null model	-109.54	225.517	12.092	0	
Litter cover	BA decline + BA decline^2	-119.17	249.446	0	0.646	No
	BA decline	-121.3	251.319	1.873	0.645	
	Null model	-159.07	324.574	75.129	0	
Grass cover	BA decline	9.434	-10.14	0	0.161	No
	BA decline + BA decline^2	9.08	-7.049	3.091	0.164	
	Null model	3.389	-0.35	9.79	0	
Palatable tree browseline	BA decline + BA decline^2	-94.72	200.979	0	0.028	No

	BA decline	-96.76	202.519	1.541	0.028	
	Null model	-98.285	203.155	2.176	0	
Unpalatable tree browseline	BA decline + BA decline^2	-112.05	235.38	0	0.035	No
	BA decline	-114.08	237.002	1.622	0.031	
	Null model	-115.98	238.449	3.069	0	
Holly cover	Null model	-66.398	139.445	0	0	No
	BA decline + BA decline^2	-64.272	140.258	0.813	0.005	
	BA decline	-65.945	141.002	1.557	0.002	
Rubus cover	BA decline + BA decline^2	-71.326	154.366	0	0.184	No
	BA decline	-73.14	155.391	1.025	0.188	
	Null model	-78.591	163.832	9.466	0	
Holly shrubs browsed	Null model	-58.867	124.163	0	0	No
	BA decline	-57.975	124.677	0.514	0.047	
	BA decline + BA decline^2	-56.907	124.926	0.763	0.059	
Rubus shrubs browsed	BA decline + BA decline^2	-73.077	157.868	0	0.129	No
	BA decline	-76.25	161.611	3.744	0.076	
	Null model	-78.612	163.873	6.005	0	
Average crown condition	BA decline	9.554	-10.177	0	0.156	No
	BA decline + BA decline^2	9.691	-7.954	2.224	0.155	
	Null model	6.921	-7.296	2.881	0	
Understorey condition	Null model	-19.867	46.35	0	0	No
	BA decline	-20.713	50.478	4.128	0.004	
	BA decline	-19.898	51.418	5.068	0.028	

	+ BA decline^2					
Canopy openness	BA decline + BA decline^2	-43.877	98.866	0	0.886	Yes
	BA decline	-49.514	107.756	8.89	0.872	
	Null model	-112.8	232.025	133.159	0	
Understorey openness	BA decline + BA decline^2	-115.73	242.573	0	0.292	No
	BA decline	-117.34	243.401	0.828	0.295	
	Null model	-130.79	268.004	25.431	0	
Tree seedling richness	BA decline	-102.42	211.273	0	0.195	No
	BA decline + BA decline^2	-102.29	213.301	2.028	0.209	
	Null model	-109.1	222.414	11.141	0	
Tree sapling richness	Null model	-62.582	129.375	0	0	No
	BA decline	-62.561	131.551	2.176	0.001	
	BA decline + BA decline^2	-62.561	133.85	4.475	0.001	
Spider species richness	BA decline	-55.813	118.769	0	0.138	No
	Null model	-57.636	119.817	1.048	0	
	BA decline + BA decline^2	-55.245	120.49	1.721	0.189	
Rove beetles species richness	Null model	-50.365	105.276	0	0	No
	BA decline + BA decline^2	-48.635	107.27	1.994	0.134	
	BA decline	-50.232	107.607	2.331	0.012	
Carabid beetles species richness	Null model	-51.53	107.606	0	0	No
	BA decline	-51.005	109.153	1.547	0.046	
	BA decline	-50.59	111.179	3.573	0.086	

	+ BA decline^2					
Ant species richness	BA decline	-37.656	82.455	0	0.484	No
	BA decline	-37.467	84.933	2.479	0.529	
	Null model	-45.428	95.401	12.946	0	
Weevil species richness	Null model	-28.533	61.611	0	0	No
	BA decline	-28.485	64.113	2.502	0.006	
	BA decline + BA decline^2	-28.165	66.33	4.719	0.048	
Woodlice species richness	Null model	-37.242	79.029	0	0	No
	BA decline	-37.226	81.595	2.566	0.002	
	BA decline + BA decline^2	-36.943	83.887	4.857	0.029	
Ground-dwelling arthropod species richness	BA decline	-69.5	146.15	0	0.264	No
	BA decline + BA decline^2	-69.28	148.56	2.41	0.283	
	Null model	-73.72	151.98	5.84	0	
Moisture content of the mineral layer	BA decline + BA decline^2	-208.68	428.469	0	0.026	No
	BA decline	-212.41	433.539	5.07	0.013	
	Null model	-214.89	436.202	7.733	0	
Moisture content of the organic layer	BA decline + BA decline^2	-300.81	612.734	0	0.005	No
	BA decline	-305.58	619.878	7.143	0.005	
	Null model	-309.38	625.194	12.46	0	
Cervus dung proportional	BA decline + BA decline^2	-2758.3	5525.3	0	0.029	No
	BA decline	-2780.3	5567.07	41.766	0.001	
	Null model	-2871.2	5746.54	221.241	0	

Equus dung proportional	BA decline	-627.11	1260.65	0	0.173	No
	BA decline + BA decline^2	-627.11	1262.95	2.298	0.175	
	Null model	-729.68	1463.57	202.92	0	
Proportional dung total	BA decline + BA decline^2	-2636.6	5281.92	0	0.016	No
	BA decline	-2647.1	5300.56	18.636	0.004	
	Null model	-2674.3	5352.8	70.88	0	
Very large beech trees (74.97 cm < dbh < 103 cm)	BA decline	-61.549	129.643	0	0.104	No
	Null model	-63.607	131.48	1.836	0	
	BA decline + BA decline^2	-61.535	132	2.356	0.101	
Large beech trees (68.32 cm < dbh < 74.97 cm)	BA decline	-59.977	126.499	0	0.294	No
	BA decline + BA decline^2	-59.857	128.644	2.145	0.322	
	Null model	-67.724	139.714	13.216	0	
Holly tree abundance	BA decline	-118.51	243.555	0	0.015	No
	BA decline + BA decline^2	-117.8	244.532	0.978	0.019	
	Null model	-120.17	244.615	1.06	0	
Beech trees abundance	BA decline + BA decline^2	-101	210.719	0	0.778	Yes
	BA decline	-111.49	229.4	18.682	0.639	
	Null model	-171.05	346.306	135.587	0	
Holly saplings abundance	BA decline + BA decline^2	-354.54	717.797	0	0.005	No
	BA decline	-360.28	726.991	9.195	0	
	Null model	-363.17	730.549	12.752	0	

Beech saplings abundance	BA decline + BA decline^2	-35.653	80.033	0	0.075	No
	BA decline	-42.921	92.27	12.236	0.008	
	Null model	-44.862	93.935	13.902	0	
Overall saplings abundance	BA decline + BA decline^2	-369.57	747.876	0	0.006	No
	BA decline	-373.97	754.369	6.493	0	
	Null model	-376.15	756.504	8.628	0	
Ground flora species richness	BA decline + BA decline^2 + log(Dung)	-183.09	377.285	0	0.596	Yes
	BA decline + log(Dung)	-186.96	382.653	5.368	0.548	
	BA decline + BA decline^2	-187.4	383.531	6.246	0.549	
	BA decline	-192.55	391.533	14.249	0.486	
	Null model	-257.45	521.336	144.052	0.028	
Woody ground flora species richness	BA decline	-112.51	231.446	0	0.052	No
	BA decline + log(Dung)	-112.4	233.532	2.087	0.055	
	BA decline + BA decline^2	-112.5	233.731	2.285	0.053	
	Null model	-113.92	234.265	2.819	0.001	
	BA decline + BA decline^2 + log(Dung)	-112.4	235.912	4.467	0.056	
	BA decline	-172.81	356.738	0	0.655	Yes

	+ BA decline^2 + log(Dung)					
Non-woody ground flora species richness	BA decline + BA decline^2	-177.13	362.98	6.242	0.61	
	BA decline + log(Dung)	-180.15	369.033	12.295	0.582	
	BA decline	-186.09	378.598	21.86	0.517	
	Null model	-262.04	530.507	173.769	0.032	
Lichen species richness	BA decline + BA decline^2 + Holly abundance	-221.1	453.317	0	0.437	Yes
	BA decline + Holly abundance	-231.85	472.417	19.1	0.331	
	Null model	-250.11	506.652	53.335	0.14	
Lichen species richness on holly	Null model	-224.964	454.138	0	0	No
	BA decline	-224.168	454.764	0.626	0.001	
	BA decline + BA decline^2	-223.993	456.712	2.574	0.004	
Lichen species richness on beech	BA decline + BA decline^2	-208.98	426.688	0	0.599	Yes
	BA decline	-238.79	484.014	57.326	0.392	
	Null model	-289.57	583.34	156.652	0	
Organic layer loss on ignition	Null model	-47.462	101.352	0	0	No
	BA decline	-47.661	104.049	2.697	0.008	
	BA decline + BA decline^2	-47.408	105.927	4.575	0.008	

Mineral layer loss on ignition	Null model	-63.385	133.199	0	0	No
	BA decline	-62.741	134.209	1.01	0.02	
	BA decline + BA decline^2	-62.18	135.47	2.271	0.02	
Organic layer nitrate concentration	Null model	-63.091	132.611	0	0	No
	BA decline + BA decline^2	-60.917	132.946	0.335	0.054	
	BA decline	-62.359	133.446	0.835	0.034	
Mineral layer nitrate concentration	Null model	-63.091	132.611	0	0	No
	BA decline + BA decline^2	-60.917	132.946	0.335	0.054	
	BA decline	-62.359	133.446	0.835	0.034	
Organic layer ammonium concentration	BA decline + BA decline^2	-235.07	481.246	0	0.052	No
	BA decline	-239.47	487.665	6.419	0.036	
	Null model	-243.47	493.374	12.128	0	
Mineral layer ammonium concentration	Null model	-43.781	93.99	0	0	No
	BA decline	-44.375	97.477	3.487	0.003	
	BA decline + BA decline^2	-43.62	98.351	4.361	0.006	
Potentially mineralisable nitrogen of the organic layer	Null model	-122.24	250.909	0	0	No
	BA decline + BA decline^2	-120.25	251.611	0.702	0.001	
	BA decline	-121.86	252.438	1.529	0.001	
Potentially mineralisable nitrogen of the mineral layer	BA decline + BA decline^2 + soil moisture	-186.84	387.27	0	0.129	No
	BA decline	-191.74	394.586	7.317	0.091	

	+ soil moisture					
	Null model	-196.92	402.558	15.289	0.014	
Understorey biomass	BA decline + BA decline^2	-137.21	288.01	0	0.38	Yes
	BA decline	-141.355	293.82	5.81	0.342	
	Null model	-142.626	293.98	5.97	0.335	

Table S4: Updated version of Table S3 with only linear and quadratic term of BA included as fixed effects.

Response variable	Model structure	Log likelihood	AICc	ΔAICc	Marginal r^2	Threshold?
Abundance of holly seedlings	BA decline + BA decline^2	-1364.38	2737.483	0	0.116	No
	BA decline	-1849.4	3705.234	967.751	0.033	
	Null model	-1895.36	3794.921	1057.438	0	
Abundance of beech seedlings	BA decline + BA decline^2	-279.394	567.515	0	0.217	Yes
	BA decline	-302.158	610.744	43.229	0.17	
	Null model	-331.657	667.524	100.009	0	
Abundance of oak seedlings	BA decline+ BA decline^2	-50.284	109.295	0	0.444	Yes
	BA decline	-58.639	123.706	14.412	0.147	
	Null model	-65.866	135.942	26.648	0	
Abundance of tree seedlings	BA decline+ BA decline^2	-1403.46	2815.65	0	0.134	No
	BA decline	-1907.55	3821.524	1005.874	0.046	
	Null model	-1970.62	3945.459	1129.809	0	
Abundance of palatable seedlings	BA decline + BA decline^2	-267.337	543.401	0	0.293	Yes
	BA decline	-296.268	598.964	55.564	0.224	
	Null model	-332.499	669.209	125.808	0	

	BA decline	-75.534	159.796	0.388	0.443	
	Null model	-93.483	193.394	33.987	0	
C/N ratio of the soil	BA decline + BA decline^2	-154.329	319.77	0	0.06	No
	BA decline	-156.799	322.325	2.555	0.056	
	Null model	-161.109	328.647	8.877	0	
Potassium exchangeable cations concentration in the mineral layer soil	Null model	76.59	-146.751	0	0	No
	BA decline	77.626	-146.525	0.225	0.099	
	BA decline + BA decline	76.035	-140.96	5.791	0.102	
Magnesium exchangeable cations concentration in the mineral layer soil	BA decline + BA decline^2	-109.12	229.352	0	0.018	No
	BA decline	-111.601	229.631	0.279	0	
	Null model	-110.582	229.891	0.539	0.018	
Sodium exchangeable cations concentration in the mineral layer soil	BA decline	112.188	-215.649	0	0.339	No
	BA decline + BA decline^2	109.859	-208.606	7.043	0.336	
	Null model	102.076	-197.722	17.926	0	
Calcium exchangeable cations concentration	BA decline + BA decline^2	15.602	-20.092	0	0.141	No

in the mineral layer soil	Null model	11.842	-17.256	2.836	0	
	BA decline	-123.252	255.303	275.395	0.056	
Manganese exchangeable cations concentration in the mineral layer soil	Null model	88.883	-171.338	0	0	No
	BA decline	85.913	-163.1	8.238	0.003	
	BA decline + BA decline^2	84.722	-158.333	13.005	0.024	
Iron exchangeable cations concentration in the mineral layer soil	BA decline + BA decline	-268.341	547.793	0	0.085	No
	BA decline	-273.18	555.087	7.294	0.072	
	Null model	-279.186	564.801	17.008	0	
Aluminium exchangeable cations concentration in the mineral layer soil	Null model	-38.524	83.476	0	0	No
	BA decline	-37.721	84.169	0.693	0.031	
	BA decline + BA decline^2	-37.576	86.262	2.786	0.031	
Availability of soil phosphorus	Null model	72.697	-138.966	0	0	No
	BA decline	69.793	-130.859	8.108	0	
	BA decline + BA decline^2	68.117	-125.122	13.844	0	
Total soil nitrogen	Null model	-61.364	129.156	0	0	No
	BA decline	-61.891	132.51	3.354	0.002	
	BA decline	-61.26	133.631	4.475	0.003	

	+ BA decline^2					
Total soil carbon	BA decline + BA decline^2	-230.653	472.418	0	0.077	No
	BA decline	-234.674	478.076	5.658	0.069	
	Null model	-240.08	486.589	14.171	0	
Net mineralisation	BA decline + BA decline^2	-120.972	253.168	0	0.065	No
	BA decline	-123.252	255.303	2.135	0.056	
	Null model	-125.972	258.414	5.246	0	
Ground flora species richness	BA decline + BA decline^2	-187.402	383.531	0	0.549	Yes
	BA decline	-192.552	391.533	8.002	0.486	
	Null model	-257.751	519.712	136.181	0	
Woody ground flora species richness	BA decline	-112.508	231.446	0	0.052	No
	Null model	-113.948	232.107	0.662	0	
	BA decline + BA decline^2	-112.502	233.731	2.285	0.053	
Non-woody ground flora species richness	BA decline + BA decline^2	-177.126	362.979	0	0.61	Yes
	BA decline + BA decline^2	-186.085	378.598	15.618	0.517	

	BA decline	-262.197	528.604	165.624	0	
Lichen species richness	BA decline + BA decline^2	-243.059	494.845	0	0.24	Yes
	BA decline	-250.311	507.05	12.205	0.169	
	Null model	-265.919	536.048	41.203	0	
Potentially mineralisable nitrogen of the mineral layer	BA decline + BA decline^2	-185.964	383.038	0	0.114	No
	BA decline	-191.192	391.112	8.074	0.068	
	Null model	-195.963	398.355	15.317	0	

Table S5: Statistics of the soil properties. Mean, standard deviation (SD), standard error (SE), and confidence interval (CI) of several soil properties across the stages of dieback.

	Percent basal area decline	N	Mean	SD	SE	CI
Clay (%)	0%	12	20.42	3.68	1.06	2.34
	25%	12	20.00	4.75	1.37	3.02
	50%	12	21.08	7.29	2.11	4.63
	75%	12	19.08	6.24	1.80	3.97
	100%	12	20.58	7.90	2.28	5.02
Sand (%)	0%	12	48.83	6.79	1.96	4.32
	25%	12	49.50	6.47	1.87	4.11
	50%	12	49.50	10.12	2.92	6.43
	75%	12	52.50	10.98	3.17	6.97
	100%	12	51.08	10.40	3.00	6.61
Silt (%)	0%	12	30.75	4.81	1.39	3.05
	25%	12	30.50	4.52	1.31	2.87
	50%	12	29.42	4.87	1.41	3.09
	75%	12	28.42	5.68	1.64	3.61
	100%	12	28.33	4.21	1.21	2.67
pH	0%	12	4.19	0.28	0.08	0.18
	25%	12	4.40	0.38	0.11	0.24
	50%	12	4.37	0.28	0.08	0.18
	75%	12	4.27	0.27	0.08	0.17
	100%	12	4.27	0.35	0.10	0.23
Moisture content (Organic layer)	0%	12	157.07	41.05	11.85	26.08
	25%	12	163.33	50.04	14.45	31.80
	50%	12	149.21	53.35	15.40	33.89
	75%	12	153.40	53.37	15.41	33.91
	100%	12	149.42	67.39	19.45	42.82
Moisture content (Mineral layer)	0%	12	27.94	4.85	1.40	3.08
	25%	12	34.58	16.45	4.75	10.45
	50%	12	29.00	4.76	1.37	3.02
	75%	12	27.68	6.67	1.93	4.24
	100%	12	27.81	5.57	1.61	3.54

Supplementary Methods: SM3. Graphs to support the space-for-time assumption

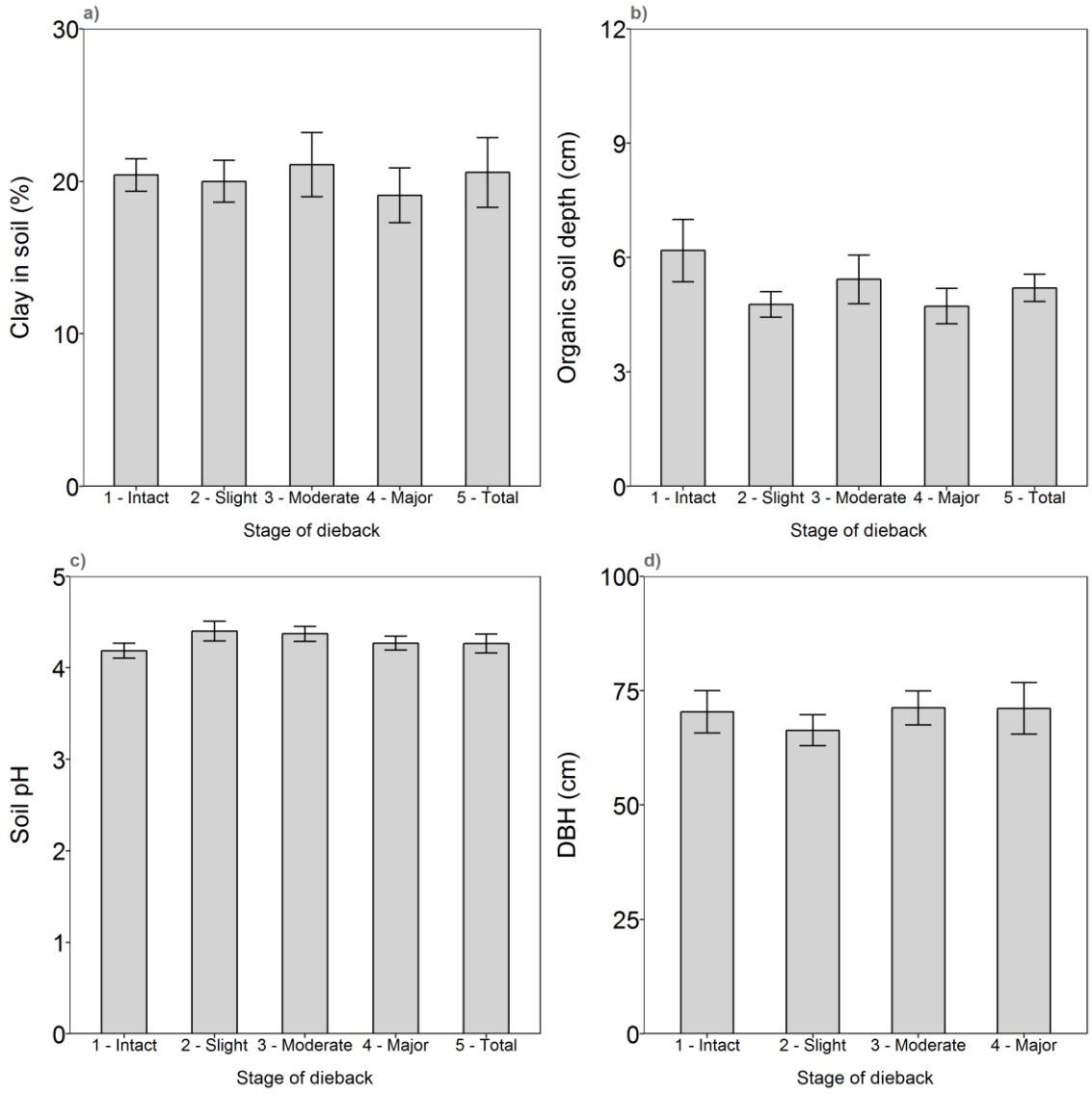


Fig S3: Mean values (n = 12) of a) clay soil content; b) depth of the organic soil layer; c) pH of the soil across the gradient of dieback; and d) diameter at breast height (DBH) of the living beech trees across the gradient of dieback. The black bars indicate the standard error of the mean.

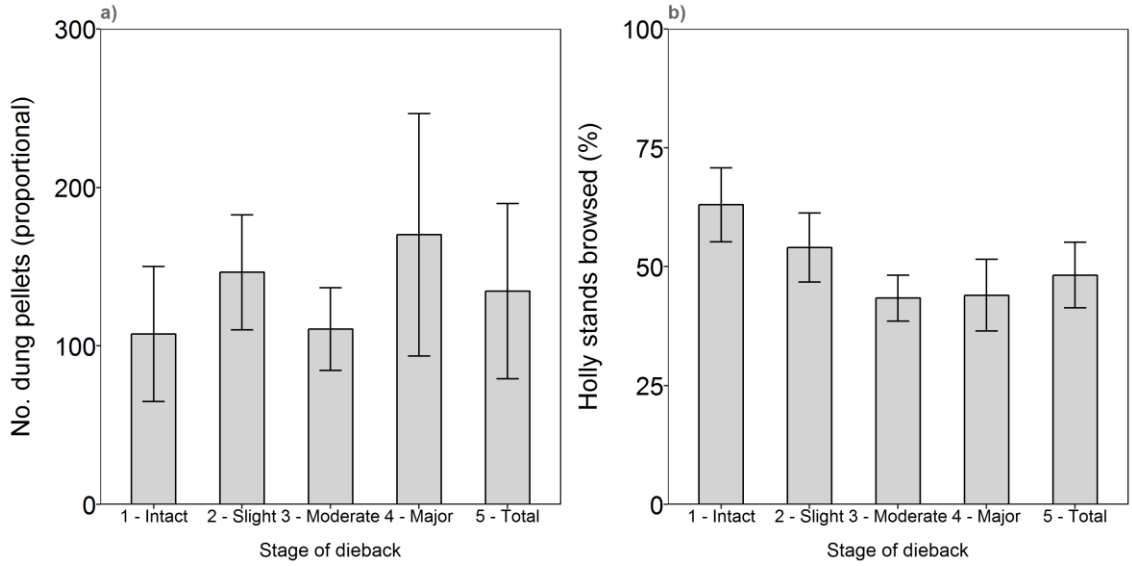


Fig S4: Mean values of a) the total herbivore dung count, and b) percentage of holly shoots browsed by herbivores across the gradient of dieback. The black bars indicate the standard error of the mean.

Supplementary references

1. Husch, B., Beers, T. W. & Kershaw, J. A. *Forest mensuration* (Wiley, 2003).
2. van Laar, A. & Akça, A. *Forest mensuration* (Springer, 2007).
3. Cantarello, E. & Newton, A. C. Identifying cost-effective indicators to assess the conservation status of forested habitats in Natura 2000 sites. *For. Ecol. Manage.* **256**, 815-826, doi:10.1016/j.foreco.2008.05.031 (2008).
4. Strickler, G. S. Use of the densiometer to estimate density of forest canopy on permanent sample plots (USDA Forest Service, 1959).
5. Jenkins, T. A. R. *et al.* FC woodland carbon code: Carbon assessment protocol (Forestry Commission, 2011).
6. McKay, H., Hudson, J. B. & Hudson, R. J. Woodfuel resource in Britain: Appendices. Fes b/w3/00787/rep/2. Dti/pub urn 03/1436 (Forestry Contracting Association, 2003).
7. Matthews, G. A. R. The carbon content of trees. Forestry commission technical paper 4 (Forestry Commission, 1993).
8. Stewart, K. E. J., Bourn, N. A. D. & Thomas, J. A. An evaluation of three quick methods commonly used to assess sward height in ecology. *J. Appl. Ecol.* **38**, 1148-1154, doi:10.1046/j.1365-2664.2001.00658.x (2001).
9. Bergström, R. & Guillet, C. Summer browsing by large herbivores in short-rotation willow plantations. *Biomass Bioenergy* **23**, 27-32, doi:10.1016/S0961-9534(02)00027-2 (2002).
10. Gibson, D. J. *Methods in comparative plant population ecology* (Oxford University Press, 2002).
11. Bazely, D. R., Myers, J. H. & da Silva, K. B. The response of numbers of bramble prickles to herbivory and depressed resource availability. *Oikos* **61**, 327-336, doi:10.2307/3545240 (1991).
12. Campbell, D., Swanson, G. M. & Sales, J. Methodological insights: Comparing the precision and cost-effectiveness of faecal pellet group count methods. *J. Appl. Ecol.* **41**, 1185-1196, doi:10.1111/j.0021-8901.2004.00964.x (2004).

13. Marques, F. F. C. *et al.* Estimating deer abundance from line transect surveys of dung: Sika deer in southern Scotland. *J. Appl. Ecol.***38**, 349-363, doi:10.1046/j.1365-2664.2001.00584.x (2001).
14. Jenkins, K. J. & Manly, B. A double-observer method for reducing bias in faecal pellet surveys of forest ungulates. *J. Appl. Ecol.***45**, 1339-1348, doi:10.1111/j.1365-2664.2008.01512.x (2008).
15. DeLuca, T., Zewdie, S., Zackrisson, O., Healey, J. & Jones, D. Bracken fern (*Pteridium aquilinum* L. Kuhn) promotes an open nitrogen cycle in heathland soils. *Plant Soil* **367**, 521-534, doi:10.1007/s11104-012-1484-0 (2013).
16. Mulvaney, R. S. Nitrogen - inorganic forms in *Methods of soil analysis. Part 3 - chemical methods* (ed. Sparks, D. L.) 1123–1184 (Soil Science Society of America, 1996).
17. Miranda, K. M., Espey, M. G. & Wink, D. A. A rapid, simple spectrophotometric method for simultaneous detection of nitrate and nitrite. *Nitric Oxide* **5**, 62-71, doi:10.1006/niox.2000.0319 (2001).
18. Keeney, D. R. in *Methods of soil analysis: Chemical and microbiological properties* (eds. Page, A. L., Miller, R. H. & Keeney, D. R.) (Soil Society of America, 1982).
19. PP Systems. EGM-4 Environmental Gas Monitor for CO_2: Operator's manual version 4.18 (PP Systems, 2010).
20. Rowell, D. L. *Soil science: Methods & application* (John Wiley & Sons, Ltd, 1994).
21. Dytham, C. *Choosing and using statistics: A biologist's guide* (John Wiley & Sons, 2011).
22. Warton, D. I. & Hui, F. K. C. The arcsine is asinine: The analysis of proportions in ecology. *Ecology* **92**, 3-10, doi:10.1890/10-0340.1 (2010).
23. Burnham, K. P. & Anderson, D. R. *Model selection and multimodel inference* (Springer-Verlag, 2002).
24. Barton, K. Mumin: Multi-model inference: R package version 1.10.0. (2014).
25. Nakagawa, S. & Schielzeth, H. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods Ecol. Evol.* **4**, 133-142 (2013).
26. Yu, D. W. *et al.* Biodiversity soup: Metabarcoding of arthropods for rapid biodiversity assessment and biomonitoring. *Methods Ecol. Evol.* **3**, 613-623, doi:10.1111/j.2041-210X.2012.00198.x (2012).
27. NBN Gateway. National Biodiversity Networks Gateway https://data.nbn.org.uk/ (2015).
28. de Jong, Y. et al. Fauna Europaea – all European animal species on the web. Biodiversity Data Journal. **2**, e4034, doi:10.3897/BDJ.2.e4034 (2014).
29. AntWeb. AntWeb https://www.antweb.org (2015)
30. British Arachnological Society. Spider and harvestman recording scheme http://srs.britishspiders.org.uk (2015).
31. Nentwig W, Blick T, Gloor D, Hänggi A, Kropf C. Spiders of Europe www.araneae.unibe.ch (2015).

Appendix 3.1: Map of the Ancient and Ornamental woodlands of the New Forest

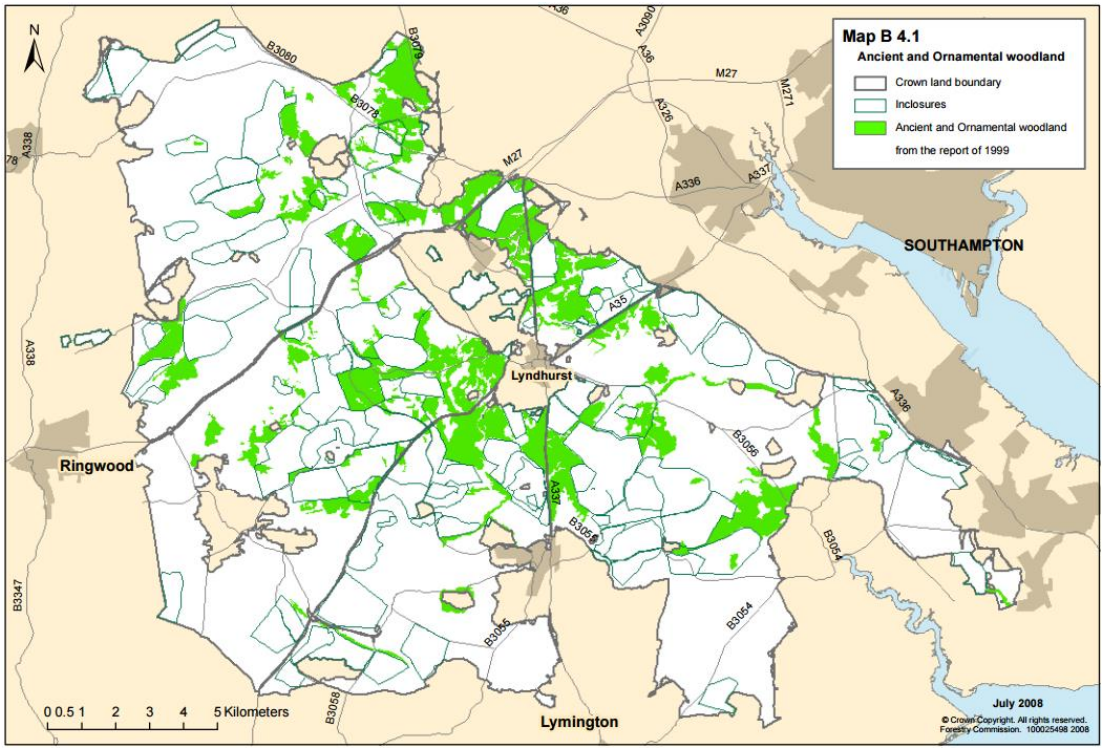


Fig. A3.1: Map of the Ancient and Ornamental woodlands (green) of the New Forest. Reproduced from Wright and Westerhoff (2001).

Appendix 3.2: The CSM assessment targets for the pasture woodlands of the New Forest

Site Name: **New Forest**	Site Unit Name/ Number:	Date Visited:
Level 1 Habitat Type: **Pasture Woodland** (Habitats Directive: Beech forests with *Ilex* and *Taxus*, rich in epiphytes (*Ilici-Fagion*), Old acidophilous oak woods with *Quercus robur* on sandy plains, Asperulo-fagetum beech forests. NVC: W15, W16, W14, W10a/W11, W10b/W11, W8b		
Condition Assessment:		
Favourable – Maintained	Unfavourable - Recovering	Partially - Destroyed
Favourable - Recovered	Unfavourable - Maintained	Destroyed
Recommended Visiting Period: Anytime		
Recommended Frequency of Visits : All Pasture Woodland units to be visited within 3 yrs		

Level 1 Attribute	**Target**	**Yes**	**No**
Area of A&O Woodland	Maintain existing area of ancient woodland on existing sites		
Regeneration (Native species only)	At least 1 native sapling (>1.5m, <15cm dbh) (excluding birch), or leader out of reach of grazing animals within 30 minutes walking.		
	Oak and Beech contributing at least 10% of the saplings seen		
	Fallen branch wood present allowing scrub and sapling development		
Composition	<1% non-native species in canopy or shrub layer.		
Natural Processes and Structural Development	No evidence of recent (within last 5 yrs) felling of native trees.		
	<1% (local) ground disturbance		
	No evidence of recent (within last 5 yrs) planting.		

	No evidence of recent (within last 5 yrs) drainage / ditch maintenance		
	No evidence of essential safety work, eg felling, drainage etc.		
	Canopy cover present over 30-90% of unit area		
Characteristic Features of Pasture Woodland	<55%trees >80cm dbh 2.5m girth showing severe stress or death attributable to disease or pollution		
	Dead wood : *Good*: 1 or 2 large fallen trees or trunks (>50cm dia) visible, plenty 5-50cm pieces in view		
	Average: 1 or 2 large pieces, little smaller material; or only smaller material (5-50cm)in view.		
	Poor: Even small material (5-50cm) scarce		
	Absent: Nothing >15cm diameter		
	Fallen dead wood classed as average to good over most of unit		
	Holly Thickets occasional or frequent NOT dominant over most of unit (<50% ground cover)		
	Ground Vegetation: <10% soil surface poached or trampled		
	<50% of vegetation more than 10cm high (except bracken)		
	<10% vegetation heavily modified, improved or exhibiting disturbed communities attributable to recreational activities.		

Appendix 3.3: The CSM assessment targets for the A&O woodlands of the New Forest

Site Name: **New Forest**	Site Unit Name and Number:	Date Visited:
Assessed by:		
Level 1 Habitat Type: **Ancient and Ornamental Woodland**		
Condition Assessment:		
Favourable	Unfavourable	Destroyed
Favourable Maintained	Unfavourable Recovering	Part Destroyed
Favourable Recovered	Unfavourable Maintained	
	Unfavourable Declining	
Recommended Visiting Period: Anytime		
Recommended Frequency of Visits : All A&O units to be visited within 6 years		

Level 1 Attribute	**Target**	**Yes**	**No**	**Samples**				
Area of A&O Woodland	Maintain Existing Areaon its current sites							
Regeneration (Native species only)	At least 1 sapling (>1.3m, <15cm dbh) Oak or Beech within 30 mins walking.							
	Oak and beech contributing at least 10% of the saplings seen							
Composition	<1% non-native species							
	<1% significant damage by squirrels							
Natural Processes and Structural Development	Felling native trees							
	>1% (local) ground disturbance							
	Planting							
	Drainage / Ditch Maintenance							
	Essential Saftey Work							
Characteristic Elements of the A&O Woodlands	Veterans Death Rate: >55%trees>80cm dbh showing severe stress or death.							

	>5% Veteran oak / beech showing severe stress or death							
	Dead wood : *Good*: 1 or 2 large fallen trunks (>50cm dia) visible, plenty 5-50cm pieces in view							
	Average: 1 or 2 large pieces, little smaller material; or only smaller material (5-50cm) in view.							
	Poor: Even small material scarce							
	Absent: Nothing >15cm diameter							
	Fallen dead wood classed as average to good over most of unit							
	Holly Thickets occasional or frequent NOT dominant over most of unit							
	Ground Vegetation: >10% soil surface poached or trampled							
	>50% of vegetation more than 60cm high (except bracken)							
	>10% vegetation heavilly modified, improved or exhibiting disturbed communities.							
Recreational Impact	<1% major paralleling of paths.							

Appendix 3.4: CSM examples for the pasture woodlands of the New Forest taken from South Wiltshire Core Strategy Interim Habitats Regulations Assessment

Criteria feature	Attribute term in guidance	Measure	Site-specific Targets	Comments	Use for CA?
Pasture Woodland NVC: W15, W16, W14, W10/11, W8. Atlantic acidophillous beech, Old acidophillous oak and Asperulo-fagetum beech forests; Invertebrate assemblages – A11 arboreal canopy A21 wood decay F11 unshaded early successional mosaic Non-vascular plants Lichen assemblages in woodpasture & parkland (Special habitat 30) Non-vascular plants Bryophyte(Mosses and liverworts) assemblages in: Western Oceanic woodland	Structure and Natural processes	Assess by field survey using structured walk and / or transects.	No evidence of recent activity (last 5 years) such as felling of native species or tree planting, artificial ground disturbance (other than small insignificant patches), new drainage ditches or their maintenance.	The pasture woodlands are under a minimum intervention management regime except for specific conservation measures (such as holly or selected tree pollarding) restoration works and essential safety works. Therefore we should accept whatever patterns of woodland develop subject to it being composed of native species and the maintenance of certain characteristic elements. Essential safety maintenance should be recorded, and while unavoidable may, if large scale, lead to a part of a unit being considered unfavourable.	Yes
Pasture Woodland NVC: W15, W16, W14, W10/11, W8. Invertebrate assemblage – A11 arboreal canopy A21 wood decay F11 unshaded early successional mosaic	Structure and Natural processes	Assess by field survey using structured walk and / or transects.	Canopy cover present over 20-90 % of stand area (except in parkland stands).	A canopy of less than 20% should be regarded as parkland, and may require restorative action.	
	Composition	Assess by field survey using structured walk and / or transects.	At least 95% of cover in any one layer of site-native species.	The objective is that the pasture woodland should consist predominantly of locally native trees and shrubs, (mainly oak, beech and holly). Scots pine does not count as native to the site.	Yes

CONSERVATION OBJECTIVE FOR THIS HABITAT / GEOLOGICAL SITE-TYPE	To maintain the PASTURE WOODLAND at The New Forest in favourable condition, with particular reference to relevant specific designated interest features. Favourable condition is defined at this site in terms of the following site-specific standards:

Criteria feature	Attribute term in guidance	Measure	Site-specific Targets	Comments	Use for CA?
	Indicators of local distinctiveness	Assess by field survey using structured walk and / or transects.	Anything over 55% of trees greater than 80cm dbh showing severe stress (premature leaf drop) or death attributable to desease or pollution should be treated as unfavourable.	If a unit contains this amount already this should be noted so that further detiorioration or recovery (if he stress is only temporary) can be assessed.	Yes
	Indicators of local distinctiveness	Assess by field survey using structured walk and / or transects.	Deadwood: Favourable when fallen dead wood is classed as average to good.	Good: 1 0r 2 large fallen trees or trunks (>50cm dia) visible, plenty 5-50cm pieces in view. Average: 1 or 2 large pieces, little smaller pieces or only smaller material (5-50cm) in view. Poor: Even small material (5-50cm) scarce. Absent: Nothing >15cm diameter.	Yes
	Indicators of local distinctiveness	Assess by field survey using structured walk and / or transects.	Holly thickets occasional or frequent but not dominant over most of unit (<50% of ground cover).	Shading by excess holly is very detrimental to ancient tree epiphyte communities.	Yes
	Indicators of local distinctiveness	Assess by field survey using structured walk and / or transects.	<10% soil surface poached or trampled	A greater amount may be indicative of over-grazing.	Yes
	Indicators of local distinctiveness	Assess by field survey using structured walk and / or transects.	<10% vegetation heavilly modified, improved or exhibiting disturbed communities attributable to recreational activities.	Includes path gravelling, multiple path creation, etc.	Yes
	Regeneration potential	Assess by field survey using structured walk and/or transects.	At least one native sapling/young tree (>1.5m high, <15cm dbh) (excluding birch) or leader out of reach of grazing anilmals seen within 30 minutes of walking; and both oak and beech contributing at least 10% of the saplings seen. Fallen branch wood present allowing scrub and sapling development.	Regeneration requires only a thin scatter of native species getting through the sapling/young tree phase. Open space for regeneration is unlikely to be lacking in any unit, nor is there likely to be a shortage of seedlings. Damage to young trees from squirrels or deer may threaten the long-term survival of many of them but as long as some are currently present then this attribute is favourable. The presence of fallen branch wood may be a critical factor in promoting regeneration in the protection it provides from grazing animals. Exclude birch regeneration from this assessment as it is not a canopy species	Yes

Appendix 3.5: The CSM assessment targets for the Generic List.

Level 1 Habitat Type: **Generic woodland**	
Condition Assessment:	
Favourable	Unfavourable
Favourable Maintained	Unfavourable Recovering
Favourable Recovered	Unfavourable Maintained
	Unfavourable Declining

Level 1 Attribute	**Target**
Area of A&O Woodland	Maintain Existing Areaon its current sites
Regeneration (Native species only)	At least 1 sapling (>1.3m, <15cm dbh) oak or beech in plot.
	Oak and beech contributing at least 10% of the saplings seen.
	At least 1 fallen branch in a plot.
	No evidence of recent activity tree planting in plot.
Composition	<1% non-native species in plot
	<1% significant damage by squirrels in plot
Natural Processes and Structural Development	Holly thickets occasional or frequent but not dominant over most of unit (<50% of ground cover).
	Canopy cover present over 20-90 % of stand area
	At least three age classes spread across the average life expectancy of the commonest trees.
	<1% ground disturbance in plot
	Lack of general safety work evidence (including felling and drainage).
Characteristic Elements of woodlands	<55%trees >80 cm dbh 2.5m girth showing severe stress or death attributable to disease or pollution
	Dead wood is classed as average to good.
	<10% soil surface poached or trampled.
	<50% of vegetation more than 10cm high (except bracken).
	<10% vegetation heavily modified, improved or exhibiting disturbed communities attributable to recreational activities.

Appendix 3.6: CSM targets met for each plot

Table A3.61: Targets each plot met using targets from all four CSM lists. Plot numbers represent the stage of dieback (1= Intact to 5 = Total dieback; see Methods for more information). Ones (numerical) represent that a target was met for that particular plot. The targets are: Nat.sap = at least one native sapling; OBSap = oak and beech saplings make up at least 10% of all saplings; Br = fallen branch present; Sq = < 10% squirrel damage; NNS = < 1% of non-native species in canopy or shrub layer; Fell = no evidence of felling present; Pl = no evidence of planting; Dr = no evidence of drainage present; SW = no signs of safety work;; GDless1 = ground disturbance < 1%; cc20 (cc30) = canopy cover between 20 (30) and 90%; TSless55 = less than 55% of trees (DBH > 80 cm) showing signs of stress due to pollution or pathogens (Incl. snags); and Age = at least three age classes spread across the average life expectancy of the commonest trees. NAs are present in the TSless55 category if trees or snags above 80 cm DBH were not present in the plot.

Plot	Nat.Sap	OBsap	Br	Sq	NNS	Fell	Pl	Dr	SW	GDless1	cc20	cc30	TSless55	Age
1	1	0	0	1	1	1	1	1	1	1	0	0	1	1
2	0	0	0	1	1	1	1	1	1	1	0	0	0	1
3	0	0	1	1	1	1	1	1	1	0	1	1	1	1
4	1	0	1	1	0	1	1	1	1	1	1	1	0	0
5	0	0	1	NA	1	1	1	1	1	1	1	1	0	0
1	1	0	0	1	1	1	1	1	1	0	0	0	0	0
2	1	0	1	1	1	1	1	1	1	1	0	0	1	1
3	1	0	0	1	0	1	1	1	1	0	1	1	0	0
4	1	0	1	0	0	1	1	1	1	0	1	1	0	0
5	1	0	1	NA	0	1	1	1	1	0	0	0	0	0
1	1	0	1	1	1	1	1	1	1	0	0	0	1	0
2	0	0	1	1	0	1	1	1	1	0	1	1	1	0
3	1	1	1	1	0	1	1	1	1	1	1	1	0	0
4	0	0	0	1	1	1	1	1	1	0	1	1	NA	0
5	0	0	0	NA	0	1	1	1	1	0	0	0	0	0
1	1	0	0	1	1	1	1	1	1	0	0	0	0	1
2	1	0	0	1	1	1	1	1	1	1	0	0	1	1
3	0	0	1	1	1	1	1	1	1	0	1	1	1	0
4	1	0	1	1	0	1	1	1	1	0	1	1	NA	1
5	1	0	1	NA	1	1	1	1	1	0	1	1	NA	0
1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
2	1	0	1	1	1	1	1	1	1	0	0	0	NA	1
3	0	0	1	1	1	1	1	1	1	0	1	1	0	0
4	0	0	1	1	1	1	1	1	1	1	1	1	0	0
5	0	0	0	NA	1	1	1	1	1	1	1	0	NA	0
1	0	0	1	1	1	1	1	1	1	1	0	0	0	1
2	0	0	0	1	1	1	1	1	1	0	1	1	0	1
3	0	0	1	1	1	1	1	1	1	0	1	1	0	0
4	0	0	0	1	1	1	1	1	1	1	1	1	0	0
5	1	0	1	NA	0	1	1	1	1	0	0	0	NA	0
1	1	0	0	1	1	1	1	1	1	1	0	0	1	1
2	1	0	1	1	1	1	1	1	1	1	1	1	NA	0
3	1	0	1	1	0	1	1	1	1	0	1	1	NA	1
4	1	0	1	1	1	1	1	1	1	1	1	1	NA	0

Table A3.62: Targets each plot met using targets from all four CSM lists. Plot numbers represent the stage of dieback (1= Intact to 5 = Total dieback; see Methods for more information). Ones (numerical) represent that a target was met for that particular plot. The targets are: DW_tot = 'average' (DWave) or 'good' (DWgood) amount of dead wood present; HS = holly thickets not dominant (holly < 50% ground cover); TRless10 = less than 10% of vegetation/ ground poached or trampled; v10/v60 = ground flora vegetation higher than 10 cm or 60 cm; and modless10 = less than 10% vegetation heavily modified, improved or exhibiting disturbed communities attributable to recreational activities.

Plot	DWgood	DWave	DWpoor	DWnone	DW_tot	HS	TRless10	v10	v60	modless10
1	0	0	1	0	0	0	1	0	0	1
2	0	1	0	0	1	0	1	0	0	1
3	0	1	0	0	1	0	1	1	0	1
4	1	0	0	0	1	0	1	1	0	1
5	1	0	0	0	1	1	1	1	0	1
1	0	0	0	0	0	0	1	0	0	1
2	0	0	1	0	0	0	1	0	0	1
3	0	1	0	0	1	0	0	0	0	1
4	1	0	0	0	1	0	0	0	0	1
5	1	0	0	0	1	1	0	1	1	1
1	0	1	0	0	1	0	0	0	0	1
2	0	0	1	0	0	0	1	0	0	1
3	0	1	0	0	1	0	1	1	0	1
4	0	1	0	0	1	0	0	0	0	1
5	1	0	0	0	1	0	0	1	0	1
1	0	0	0	0	0	0	0	0	0	1
2	0	1	0	0	1	0	1	0	0	1
3	0	1	0	0	1	1	0	0	0	1
4	0	1	0	0	1	1	0	1	0	1
5	1	0	0	0	1	1	0	1	0	1
1	0	0	1	0	0	0	0	0	0	1
2	0	1	0	0	1	0	0	0	0	1
3	1	0	0	0	1	0	1	0	0	1
4	1	0	0	0	1	0	1	1	0	1
5	0	0	1	0	0	0	1	1	0	1
1	0	1	0	0	1	0	1	0	0	1
2	0	1	0	0	1	0	0	0	0	1
3	0	1	0	0	1	0	1	0	0	1
4	1	0	0	0	1	1	1	1	0	1
5	0	1	0	0	1	NA	1	0	0	0
1	0	0	1	0	0	0	1	0	0	1
2	0	0	1	0	0	1	1	0	0	1
3	0	1	0	0	1	1	1	1	0	1
4	0	1	0	0	1	1	1	0	0	1
5	0	1	0	0	1	0	0	1	0	1
1	0	1	0	0	1	0	1	0	0	1

Appendix 3.7: Non-CSM indicator ANOVA results for Chapter 3

Table A3.7: ANOVA results for each non-CSM indicator across the stages of woodland dieback. *p-values* shown in bold are considered are significant to the alpha level of 0.05. 'Indicator use?' indicates whether the non-CSM metric could be used as an indicator. See CD3.2 for full results.

Non-CSM metric	**Unit**	X^2	***Df***	***p*-value**	**Indicator use?**
Grass cover	% ground cover	19.898	4	**0.001**	Possible
Litter cover	% ground cover	172.034	4	**<0.001**	Possible
Moss cover	% ground cover	13.898	4	**0.008**	Possible
Bare ground	% ground cover	17.577	4	**0.001**	Possible
Bare ground and moss	% ground cover	15.539	4	**0.004**	Possible
Bracken	% ground cover	31.894	4	**<0.001**	Possible
Understorey openness	% sky visible	28.216	4	**<0.001**	Possible
Canopy openness	% sky visible	1005.977	4	**<0.001**	Possible
Ambient temperature	°C	42.229	4	**<0.001**	Possible
Soil temperature	°C	18.487	4	**0.001**	Possible
Ca:Al ratio	Ca:Al ratio	16.451	4	**0.002**	Possible
Sward height	cm	70.271	4	**<0.001**	Possible
Calcium CEC	cmol(+)/kg	11.386	4	**0.023**	Possible
CN ratio	CN ratio	9.59	4	**0.048**	Possible
Beech abundance	Individuals 0.04 ha^{-1}	180.568	4	**<0.001**	Possible
Total seedling abundance	Individuals 0.04 ha^{-1}	14.239	4	**0.007**	Possible
Holly seedling abundance	Individuals 0.04 ha^{-1}	14.225	4	**0.007**	Possible

Beech dead wood volume	$m^3 ha^{-1}$	37.086	4	**<0.001**	Possible
Lying dead wood total	$m^3 ha^{-1}$	40.151	4	**<0.001**	Possible
Electrical conductivity	$mS\ m^{-1}$	9.573	4	**0.048**	Possible

Appendix 3.8: ANOVA results comparing condition scores at each dieback stage

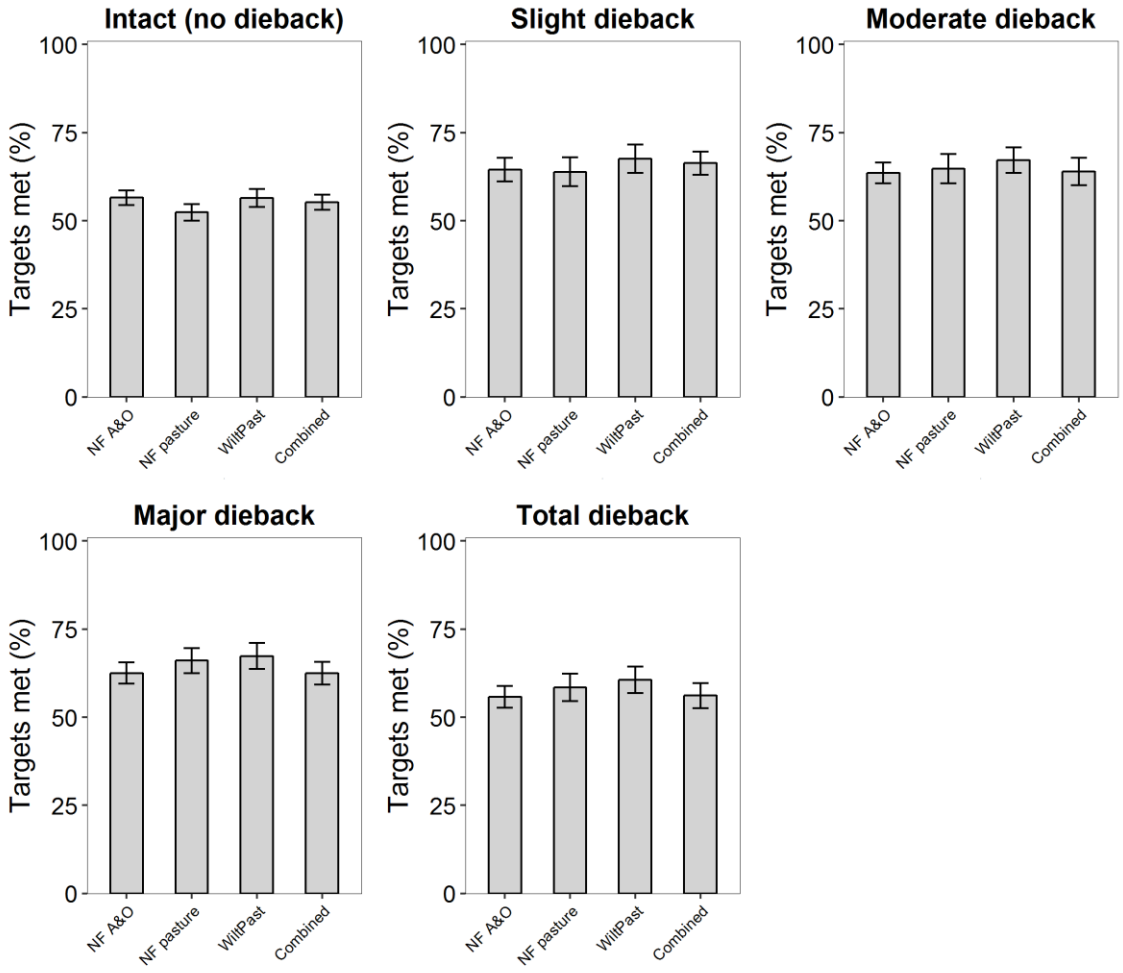


Fig. A3.8: Mean values of the percentage of targets that were met from each CSM target list at each stage of dieback. Target lists are: New Forest A&O woodlands (NF A&O), New Forest pasture woodlands (NF pasture), WiltPast, and the Generic List (Combined). For specifics of the individual CSM target lists, see text (section 3.3.3) and CD, CD3.1. The black bars indicate the standard error of the mean.

Table A3.8: Kruskal-Wallis one-way ANOVA results for the condition scores for each CSM targets lists at each stage of dieback.

Dieback stage	df	X^2	*p-value*
1 – Intact	3	1.965	0.58
2 – Slight	3	0.684	0.877
3 - Moderate	3	0.529	0.913
4 – Major	3	2.182	0.536
5 – Total	3	1.469	0.689

Appendix 4.1: Quasi-Poisson and negative binomial distributions

When data are over-dispersed, there are generally two options within ecology: using a i) quasi-Poisson (QP) or ii) using a negative binomial (NB) model (ver Hoef and Boveng, 2007). Both of these approaches use a quasi-likelihood, which means that instead of using a certain probability distribution of the data, rather a relationship between the mean and variance is specified by an additional over-dispersion parameter. Both models use weighted least squares, which are inversely proportional to the variance, and therefore weight observations differently. For QP models, weights are directly proportional to the mean, whereas for NB, weights exhibit a concave relationship with the mean (ver Hoef and Boveng, 2007).

Appendix 4.2: Comparisons of the field-collected data from the two transects for Chapter 4

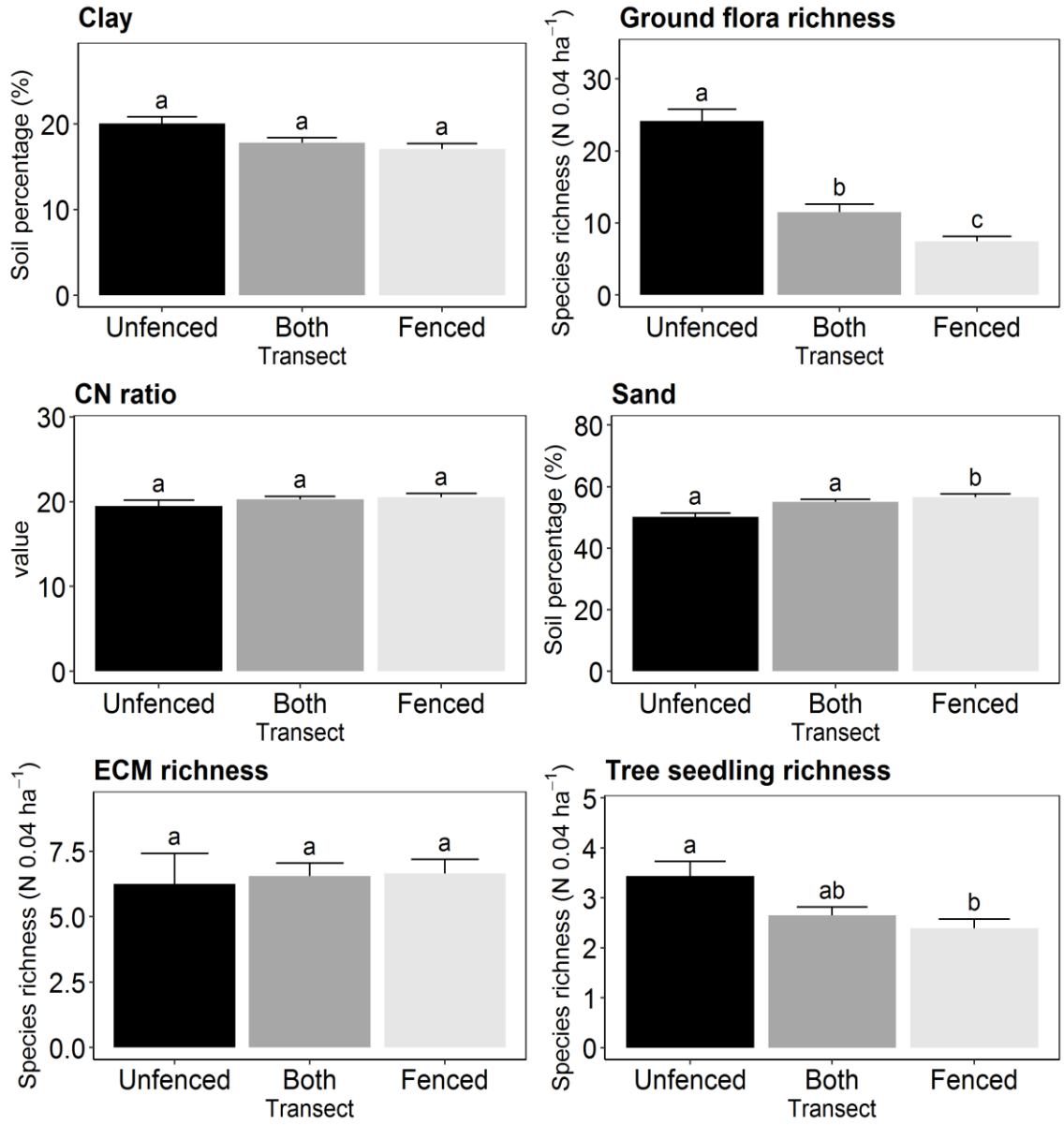


Fig. A4.21: Mean values of different field-collected variables from the Denny Wood transects. The black bars indicate the standard error of the mean. Means grouped by the same letter are not significantly different ($p < 0.05$, Tukey HSD test).

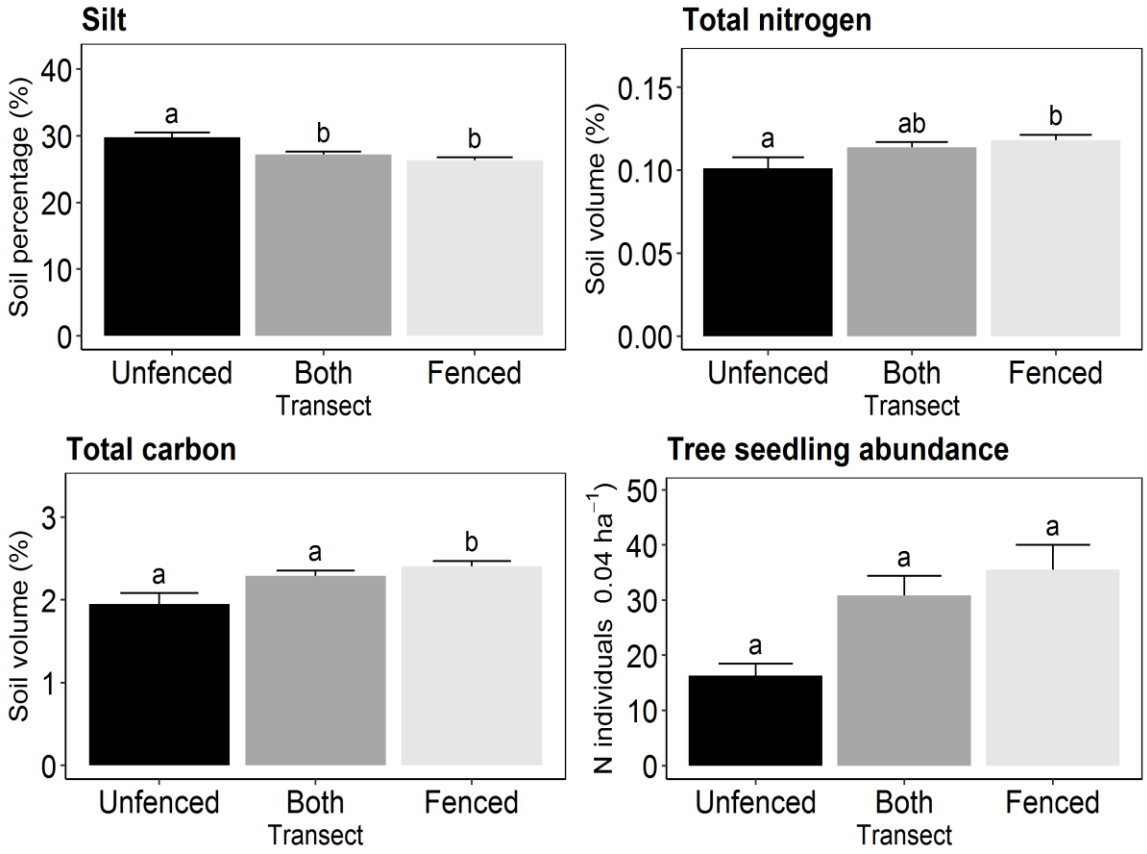


Fig. A4.22: Mean values of different field-collected variables from the Denny Wood transects. The black bars indicate the standard error of the mean. Means grouped by the same letter are not significantly different ($p < 0.05$, Tukey HSD test).

Appendix 4.3: Relationships of field-collected condition measures to all returns lidar-derived structural metrics for Chapter 4.

Table A4.31a: Relationships of field-collected condition measures for both transects from 2014 to lidar-derived all returns (AR) metrics from 2010 lidar point cloud data. Values shown in bold are considered substantial relationships based on fitting the criteria of ΔAIC > 4 from the null model and if the $r^2 > 0.4$. Null indicates that the null model was the most parsimonious.

Both transects		**Lidar metrics (AR)**									
Field data		AH	CC	CP	Ground	H50	H95	MH	Over	SDH	Under	VDR
Ground flora richness	Model	**Non-linear**	**Non-linear**	**Linear**	**Non-linear**	**Non-linear**	**Non-linear**	**Non-linear**	**Non-linear**	Null	**Non-linear**	**Non-linear**
	r^2	**0.7**	**0.68**	**0.63**	**0.67**	**0.69**	**0.65**	**0.65**	**0.68**	-	**0.66**	**0.7**
	ΔAIC	**102**	**81.62**	**13.48**	**71.36**	**90.58**	**40.28**	**35**	**84.05**	-	**47.8**	**102.99**
ECM richness	Model	Non-linear	Non-linear	Non-linear	Non-linear	Non-linear	Non-linear	Null	Non-linear	Non-linear	Non-linear	Non-linear
	r^2	0.1	0.15	0.08	0.11	0.11	0.06	-	0.14	0.09	0.06	0.12
	ΔAIC	20	51.43	7.82	23.38	28.75	2.29	-	42.37	14.92	1.08	29.15
Seedling richness	Model	Non-linear	Non-linear	Non-linear	Non-linear	Linear	Non-linear	Linear	Non-linear	Linear	Non-linear	Non-linear
	r^2	0.33	0.28	0.14	0.31	0.26	0.29	0.23	0.27	0.09	0.19	0.31
	ΔAIC	67.41	53.16	12.29	62	5.93	56.91	42.6	51	1.15	26.52	64
Seedlings abundance	Model	Non-linear	Non-linear	Linear	Non-linear	Non-linear	Non-linear	Null	Non-linear	Non-linear	Non-linear	Non-linear
	r^2	0.27	0.29	0.25	0.26	0.29	0.2	-	0.29	0.19	0.26	0.31
	ΔAIC	49.47	67.56	44.02	48.87	64.02	8.25	-	66.87	2.8	49.02	80.81
Soil N	Model	Linear	Linear	Non-linear	Linear	Linear	Linear	Linear	Linear	Non-linear	Non-linear	Linear
	r^2	0.07	0.03	0.03	0.02	0.07	0.12	0.11	0.04	0.09	0.19	0.06
	ΔAIC	32.06	14.85	10.19	10.02	30.27	51.35	46.46	19.61	37.48	96.57	26.08
Soil C	Model	Linear	Linear	Linear	Linear	Linear	Linear	Linear	Linear	Null	Non-linear	Linear
	r^2	0.14	0.1	0.1	0.07	0.12	0.12	0.09	0.1	-	0.21	0.1
	ΔAIC	65.23	45.36	45.84	35.54	52.57	50.82	39.45	49.78	-	109.3	48.21

Table A4.31b: Relationships of field-collected condition measures for both transects from 2014 to lidar-derived all returns (AR) metrics from 2010 lidar point cloud data. Values shown in bold are considered substantial relationships based on fitting the criteria of ΔAIC > 4 from the null model and if the r^2 > 0.4. Null indicates that the null model was the most parsimonious.

CN Ratio	Model	Linear	Linear	Non-linear	Linear	Linear	Null	Non-linear	Linear	Non-linear	Non-linear	Non-linear
	r^2	0.02	0.04	0.1	0.03	0.01	-	<0.01	0.03	0.11	<0.01	0.02
	ΔAIC	13.09	22.01	39.43	23.01	6.58	-	1.93	19.33	46.87	1.05	8.41
Clay	Model	Linear	Non-linear	Linear	Non-linear	Non-linear	Non-linear	Linear	Non-linear	Non-linear	Non-linear	Non-linear
	r^2	0.15	0.22	0.14	0.2	0.11	0.04	0.02	0.21	0.22	0.08	0.23
	ΔAIC	33.02	45.46	24.53	34.72	21.03	7.97	1.09	40.98	103.42	7.03	77.79
Silt	Model	Linear	Non-linear	Non-linear	Non-linear	Linear	Non-linear	Linear	Non-linear	Non-linear	Non-linear	Linear
	r^2	0.22	0.22	0.06	0.2	0.19	0.17	0.11	0.22	0.02	0.11	0.17
	ΔAIC	64.05	56.43	6.19	50.29	51.64	60.66	39.91	53.62	17.48	15.3	41.95
Sand	Model	Linear	Non-linear	Linear	Non-linear	Linear	Linear	Non-linear	Non-linear	Non-linear	Non-linear	Linear
	r^2	0.22	0.27	0.12	0.21	0.17	0.09	0.07	0.26	0.13	0.12	0.17
	ΔAIC	104.1	138.61	52.91	101.113	77.15	40.32	27.35	128.34	69.07	47.78	74.7
Bulk density	Model	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null
	r^2	-	-	-	-	-	-	-	-	-	-	-
	ΔAIC	-	-	-	-	-	-	-	-	-	-	-

Table A4.32a: Relationships of field-collected condition measures for the fenced transect from 2014 to lidar-derived all returns (AR) metrics from 2010 lidar point cloud data. Values shown in bold are considered substantial relationships based on fitting the criteria of ΔAIC > 4 from the null model and if the r^2 > 0.4. Null indicates that the null model was the most parsimonious.

Fenced transect		**Lidar metrics (AR)**										
Field data		AH	CC	CP	Gr	H50	H95	MH	Over	SDH	Under	VDR
Ground flora richness	Model	**Linear**	**Linear**	Null	**Linear**	Linear	Null	Null	**Linear**	Null	Null	Linear
	r^2	**0.44**	**0.44**	-	**0.44**	0.42	-	-	**0.43**	-	-	0.44
	ΔAIC	**5.82**	**5.62**	-	**5.66**	4.39	-	-	**5.31**	-	-	6.18
ECM richness	Model	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null
	r^2	-	-	-	-	-	-	-	-	-	-	-
	ΔAIC	-	-	-	-	-	-	-	-	-	-	-
Seedling richness	Model	Linear	Linear	Null	Linear	Non-linear	Linear	Linear	Linear	Null	Null	Linear
	r^2	0.27	0.3	-	0.27	0.27	0.21	0.16	0.27	-	-	0.26
	ΔAIC	6.15	7.11	-	6.24	49.95	4.28	2.66	6.26	-	-	5.86
Seedlings abundance	Model	Non-linear	Non-linear	Linear	Non-linear	Non-linear	Linear	Null	Non-linear	Null	Linear	Non-linear
	r^2	0.3	0.28	0.18	0.28	0.29	0.17	-	0.28	-	0.22	0.33
	ΔAIC	7.13	6.13	2.33	6.65	6.43	2.48	-	6.81	-	3.47	9.23
Soil N	Model	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null
	r^2	-	-	-	-	-	-	-	-	-	-	-
	ΔAIC	-	-	-	-	-	-	-	-	-	-	-
Soil C	Model	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null
	r^2	-	-	-	-	-	-	-	-	-	-	-
	ΔAIC	-	-	-	-	-	-	-	-	-	-	-

Table A4.32b: Relationships of field-collected condition measures for the fenced transect from 2014 to lidar-derived all returns (AR) metrics from 2010 lidar point cloud data. Values shown in bold are considered substantial relationships based on fitting the criteria of ΔAIC > 4 from the null model and if the r^2 > 0.4. Null indicates that the null model was the most parsimonious.

Fenced transect		**Lidar metrics (AR)**										
Field data		AH	CC	CP	Gr	H50	H95	MH	Over	SDH	Under	VDR
CN Ratio	Model	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null
	r^2	-	-	-	-	-	-	-	-	-	-	-
	ΔAIC	-	-	-	-	-	-	-	-	-	-	-
Clay	Model	Linear	Linear	Linear	Linear	Null	Null	Null	Linear	**Non-linear**	Null	Null
	r^2	0.32	0.34	0.33	0..33	-	-	-	0.34	**0.56**	-	-
	ΔAIC	2.35	3.95	2.31	2.21	-	-	-	3.44	**19.64**	-	-
Silt	Model	Null	Linear	Null	Null	Null	Null	Null	Null	Non-linear	Null	Null
	r^2	-	0.33	-	-	-	-	-	-	0.11	-	-
	ΔAIC	-	4.25	-	-	-	-	-	-	4.03	-	-
Sand	Model	Linear	Non-linear	Null	Linear	Non-linear	Null	Null	Non-linear	Non-linear	Null	Null
	r^2	0.1	0.17	-	0.11	0.29	-	-	0.15	0.39	-	-
	ΔAIC	2.23	4.2	-	3.19	5.76	-	-	3.02	19.06	-	-
Leaf discolouration	Model	Non-linear	**Non-linear**	**Non-linear**	Null	Non-linear	Linear	Linear	**Non-linear**	Non-linear	Null	Non-linear
	r^2	0.37	**0.88**	**0.47**	-	0.38	0.15	0.17	**0.54**	0.16	-	0.21
	ΔAIC	17.22	**43.47**	**31.92**	-	28.27	3.04	2.85	**28.11**	5.32	-	6.5
Leaf loss	Model	**Non-linear**	**Non-linear**	Non-linear	Null	Non-linear	Linear	Linear	**Non-linear**	Non-linear	Non-linear	Null
	r^2	**0.67**	**0.92**	0.42	-	0.17	0.07	0.07	**0.92**	0.12	0.04	-
	ΔAIC	**38.48**	**49.49**	34.99	-	8.96	5.79	6.67	**50.8**	10.7	3.23	-

Table A4.32c: Relationships of field-collected condition measures for the fenced transect from 2014 to lidar-derived all returns (AR) metrics from 2010 lidar point cloud data. Values shown in bold are considered substantial relationships based on fitting the criteria of ΔAIC > 4 from the null model and if the r^2 > 0.4. Null indicates that the null model was the most parsimonious.

Fenced transect		**Lidar metrics (AR)**										
Field data		AH	CC	CP	Gr	H50	H95	MH	Over	SDH	Under	VDR
Structural crown loss	Model	**Null**	**Null**	Null	Null	Null	Null	Null	**Null**	Linear	Null	Null
	r^2	-	-	-	-	-	-	-	-	0.04	-	-
	ΔAIC	-	-	-	-	-	-	-	-	2.5	-	-
Browseline	Model	Null	Linear	Non-linear	Linear	Null	Null	Linear	Null	Non-linear	Non-linear	Null
	r^2	-	0.05	0.22	0.04	-	-	0.04	-	0.08	0.09	-
	ΔAIC	-	1.46	11.24	1.48	-	-	1.85	-	3.52	2.92	-
Crown condition	Model	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null
	r^2	-	-	-	-	-	-	-	-	-	-	-
	ΔAIC	-	-	-	-	-	-	-	-	-	-	-
Bulk density	Model	Null	Null	Null	Null	Non-linear	Null	Linear	Null	Null	Linear	Non-linear
	r^2	-	-	-	-	0.08	-	0.03	-	-	0.04	0.06
	ΔAIC	-	-	-	-	3.94	-	1.25	-	-	1.74	0.81
Pony dung	Model	Null	Null	Null	Null	Null	Null	Null	Null	Null	Non-	Null
	r^2	-	-	-	-	-	-	-	-	-	0.24	-
	ΔAIC	-	-	-	-	-	-	-	-	-	4.39	-
Deer dung	Model	Non-linear	Non-linear	Non-linear	Null	Non-linear	Linear	Linear	Non-linear	Non-linear	Null	Null
	r^2	0.32	0.91	0.61	-	0.26	0.07	0.05	0.92	0.12	-	-
	ΔAIC	16.2	42.13	34.52	-	17.2	4.7	2.51	43.05	9.09	-	-

Table A4.33a: Relationships of field-collected condition measures for the unfenced transect from 2014 to lidar-derived all returns (AR) metrics from 2010 lidar point cloud data. Values shown in bold are considered substantial relationships based on fitting the criteria of ΔAIC > 4 from the null model and if the r^2 > 0.4. Null indicates that the null model was the most parsimonious.

Unfenced transect		**Lidar metrics (FR)**										
Field data		AH	CC	CP	Ground	H50	H95	MH	Over	SDH	Under	VDR
Ground flora richness	Model	Null	Non-linear	Null	Null	Null	Null	Null	Null	Null	Linear	Non-linear
	r^2	-	0.5	-	-	-	-	-	-	-	0.47	0.49
	ΔAIC	-	3.2	-	-	-	-	-	-	-	1.66	2.54
ECM richness	Model	Linear	**Linear**	Null	**Linear**	Null	Null	Null	Null	Null	Linear	Non-linear
	r^2	0.26	**0.36**	-	**0.45**	-	-	-	-	-	0.34	0.53
	ΔAIC	21.29	**11.58**	-	**15.6**	-	-	-	-	-	10.35	1.57
Seedling richness	Model	Null	Null	Null	Null	Null	Null	Null	Null	Null	Linear	Null
	r^2	-	-	-	-	-	-	-	-	-	0.49	-
	ΔAIC	-	-	-	-	-	-	-	-	-	3.04	-
Seedlings abundance	Model	Null	Null	Null	Null	Null	Linear	**Non-linear**	Null	Linear	**Non-linear**	Null
	r^2	-	-	-	-	-	0.28	**0.44**	-	0.3	**0.63**	-
	ΔAIC	-	-	-	-	-	8.26	**14.33**	-	9.3	**27.8**	-
Soil N	Model	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null
	r^2	-	-	-	-	-	-	-	-	-	-	-
	ΔAIC	-	-	-	-	-	-	-	-	-	-	-
Soil C	Model	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null	Null
	r^2	-	-	-	-	-	-	-	-	-	-	-
	ΔAIC	-	-	-	-	-	-	-	-	-	-	-

Table A4.33b: Relationships of field-collected condition measures for the unfenced transect from 2014 to lidar-derived all returns (AR) metrics from 2010 lidar point cloud data. Values shown in bold are considered substantial relationships based on fitting the criteria of ΔAIC > 4 from the null model and if the r^2 > 0.4. Null indicates that the null model was the most parsimonious.

Unfenced transect		**Lidar metrics (FR)**										
Field data		AH	CC	CP	Ground	H50	H95	MH	Over	SDH	Under	VDR
CN.Ratio	Model	Null	Null	Null	Null	Null	Non-linear	Null	Null	Non-linear	Null	Null
	r^2	-	-	-	-	-	0.34	-	-	0.21	-	-
	ΔAIC	-	-	-	-	-	8.05	-	-	2.11	-	-
Clay	Model	Non-linear	Linear	Null	Linear	Non-linear	Null	**Null**	Non-linear	Null	Null	Non-linear
	r^2	0.21	0.14	-	0.258	0.17	-	-	0.24	-	-	0.17
	ΔAIC	2.74	2.17	-	7.85	1.36	-	-	3.73	-	-	0.95
Silt	Model	Non-linear	**Null**	**Linear**	**Non-linear**	Null	Null	**Non-linear**	Non-linear	Null	Non-linear	Null
	r^2	0.42	-	**0.52**	**0.32**	-	-	**0.54**	0.46	-	0.41	-
	ΔAIC	5.87	-	**14.93**	**0.76**	-	-	**13.75**	8.2	-	5.5	-
Sand	Model	Non-linear	Linear	Linear	**Non-linear**	Null	Null	Null	Non-linear	Null	Non-linear	**Non-linear**
	r^2	0.33	0.2	0.22	**0.35**	-	-	-	0.39	-	0.25	**0.31**
	ΔAIC	8.08	4.92	5.7	**9.03**	-	-	-	10.74	-	3.89	**6.65**

Appendix 5.1: Tree species parameters for LANDIS-II

Table A5.1: Tree species parameter table that was used for LANDIS-II simulations for Chapter 5. Longevity is the species maximum age; sexual maturity is the age the species reaches sexual maturity; shade and fire tolerance are ranked 1 (lowest)-5 (highest); effective and maximum seed dispersal are the effective and maximum distances at which the species disperse seeds; and vegetative reproduction probability is the probability that the species resprouts, which is followed by the minimum and maximum age.

Scientific name	Common name	Longevity (yrs)	Sexual maturity (yrs)	Shade tolerance	Fire tolerance	Seed dispersal distance (m)		Vegetative reproduction probability	Resprouting age (yrs)	
						Effective	Maximum		Min	Max
Acer campestre	Field Maple	200	10	3	1	80	120	1	10	120
Acer pseudoplatanus	Sycamore	150	12	4	1	120	400	1	10	100
Alnus glutinosa	Common elder	250	12	3	1	120	200	1	10	200
Betula pendula	Silver birch	160	18	2	1	200	1600	1	10	120
Calluna Vulgaris	Ling heather	30	1	4	1	100	700	1	0	30
Carpinus betulus	Hornbeam	250	20	4	1	90	700	1	10	150
Castanea sativa	Sweet chestnut	300	35	3	1	300	700	1	10	250
Corylus avellana	Common hazel	80	10	4	1	300	700	1	10	80
Crataegus monogyna	Hawthorn	150	4	2	1	300	700	1	10	100
Fagus sylvatica	European beech	500	55	5	1	300	700	1	10	300
Frangula alnus	Alder buckthorn	80	3	2	2	300	700	1	10	30
Fraxinus excelsior	Common ash	200	17	3	1	90	120	1	10	200
Ilex aquifolium	Holly	300	10	3	1	300	700	1	10	300
Malus sylvatica	Crabapple	130	8	2	1	300	700	1	10	100
Populus alba	White poplar	250	7	2	1	500	1600	1	10	250
Prunus spinosa	Blackthorn	60	4	2	1	300	700	1	10	60
Quercus robur	Pendunculate oak	500	60	2	1	300	700	1	10	400
Quercus rubra	Red oak	200	22	4	3	300	700	0	0	0
Salix cinerea	Grey willow/ sallow	90	35	2	1	1000	1600	1	10	70
Sorbus aria	Whitebeam	150	6	2	1	300	700	0	0	0
Sorbus aucuparia	Rowan	100	15	2	1	300	700	1	10	100
Sorbus torminalis	Wild service	100	13	4	1	300	700	1	10	100
Taxus baccata	Common yew	3000	20	4	1	300	700	0	0	0
Ulex europeus	European gorse	40	2	4	1	120	700	1	0	40
Viburnum opulus	Guelder rose	50	5	2	1	300	700	1	10	40

Appendix 5.2: Effect of woodland cover on resilience with 0% WC excluded

Effect of woodland cover on resistance

WC had an effect on the resistance of six EPs under scenarios PDI1, PDI2, PDI3 and PDI4. Thus, WC influenced the resistance of 24/40 EPs altogether when there was a pulse disturbance. When there was no pulse disturbance (i.e. PDI0), WC had a significant effect on two EPs between 15 and 20 years (Table A5.21; Figs A5.21–5.24).

Table A5.21: The most parsimonious models for resistance and associated measures of parsimony (Log likelihood, AIC), support (ΔAIC, AIC weight) and goodness of fit (r^2_{adj}) with 0% WC excluded. WC and WC^2 indicate that linear and quadratic terms of woodland cover were used in the most parsimonious models, respectively. Null indicates that the null model was the most parsimonious. PDI indicates the intensity of disturbance the ecosystem properties were measured in response to.

Resistance					
Ecosystem property	**Model structure**	**Log likelihood**	**ΔAIC**	**AIC Weight**	r^2_{adj}
PDI1					
AGB	$WC+WC^2$	-6.279	49.180	1.000	0.973
Carbon	$WC+WC^2$	-1.902	60.978	1.000	0.984
ECM	$WC+WC^2$	-6.455	29.457	1.000	0.936
GF	Null	789.398	0.000	1.000	0.000
Lichen	$WC+WC^2$	-12.014	23.402	1.000	0.913
Net min	Null	789.398	0.000	1.000	0.000
Nitrogen	WC	2.639	1.295	0.607	0.488
SRR	$WC+WC^2$	14.586	54.794	1.000	0.982
Timber	WC	-7.543	26.781	1.000	0.821
Tree species	Null	-37.030	0.000	0.761	0.000
PDI2					
AGB	$WC+WC^2$	-16.838	4.983	0.923	0.800
Carbon	$WC+WC^2$	-22.526	0.234	0.528	0.743
ECM	$WC+WC^2$	-12.064	23.812	1.000	0.914
GF	Null	789.398	0.000	1.000	0.000
Lichen	$WC+WC^2$	-9.624	23.627	1.000	0.915
Net min	Null	789.398	0.000	1.000	0.000
Nitrogen	$WC+WC^2$	28.344	7.925	0.910	0.878
SRR	$WC+WC^2$	-12.602	32.185	1.000	0.940
Timber	WC	-7.115	26.644	1.000	0.821
Tree species	Null	-27.521	0.000	0.997	0.000
PDI3					

AGB	WC+WC^2	16.903	89.683	1.000	0.996
Carbon	WC+WC^2	4.619	40.195	1.000	0.963
ECM	WC+WC^2	11.313	59.029	1.000	0.985
GF	Null	789.398	0.000	1.000	0.000
Lichen	WC+WC^2	18.635	67.377	1.000	0.990
Net min	Null	789.398	0.000	1.000	0.000
Nitrogen	WC+WC^2	-0.815	26.246	1.000	0.930
SRR	WC+WC^2	9.917	63.765	1.000	0.987
Timber	Null	-22.627	0.000	0.918	0.000
Tree species	Null	-7.784	0.000	0.992	0.000
PDI4					
AGB	WC+WC^2	12.319	94.113	1.000	0.997
Carbon	WC+WC^2	22.649	68.162	1.000	0.991
ECM	WC+WC^2	25.121	82.895	1.000	0.995
GF	Null	789.398	0.000	1.000	0.000
Lichen	WC+WC^2	41.633	107.738	1.000	0.999
Net min	Null	789.398	0.000	1.000	0.000
Nitrogen	WC+WC^2	13.344	60.006	1.000	0.985
SRR	WC+WC^2	22.886	85.470	1.000	0.996
Timber	Null	780.795	0.000	1.000	0.000
Tree species	WC+WC^2	-18.538	2.907	0.806	0.778
PDI0					
AGB	Null	789.398	0.000	1.000	0.000
Carbon	Null	789.398	0.000	1.000	0.000
ECM	Null	789.398	0.000	1.000	0.000
GF	WC+WC^2	10.471	51.574	1.000	0.979
Lichen	Null	789.398	0.000	1.000	0.000
Net min	WC+WC^2	12.068	48.406	1.000	0.976
Nitrogen	Null	789.398	0.000	1.000	0.000
SRR	Null	789.398	0.000	1.000	0.000
Timber	Null	789.398	0.000	1.000	0.000
Tree species	Null	-38.783	0.000	0.555	0.000

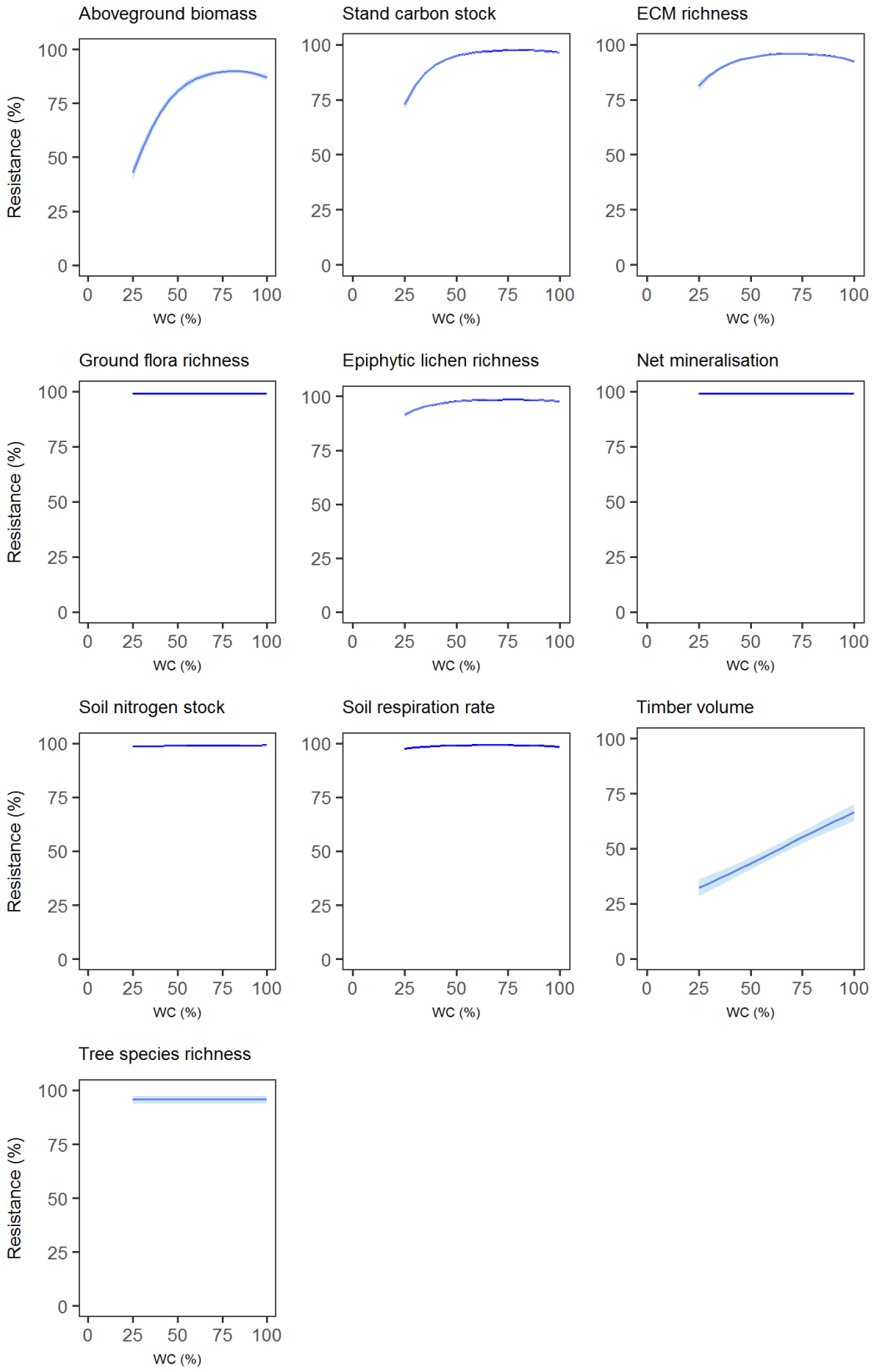


Fig. A5.21. Results of the most parsimonious GLMs for resistance of the different ecosystem properties across the woodland cover (WC) gradient resulting from PDI1 with 0% WC excluded. The blue lines represent the most parsimonious model for all EPs, and the blue surrounds represent the 95% confidence intervals of the most parsimonious model.

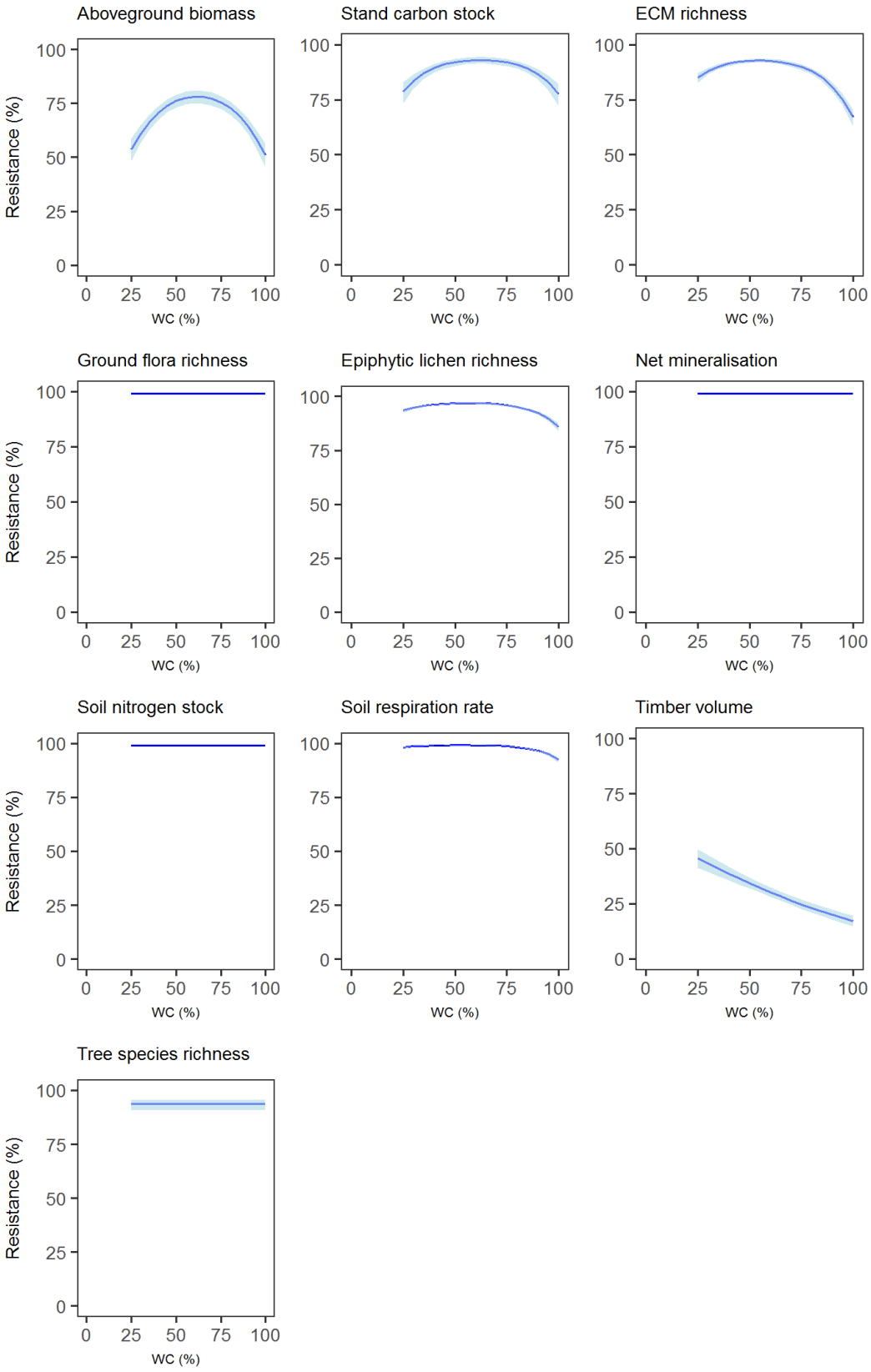


Fig. A5.22. Results of the most parsimonious GLMs for resistance of the different ecosystem properties across the woodland cover (WC) gradient resulting from PDI2 with 0% WC excluded. The blue lines represent the most parsimonious model for all EPs, and the blue surrounds represent the 95% confidence intervals of the most parsimonious model.

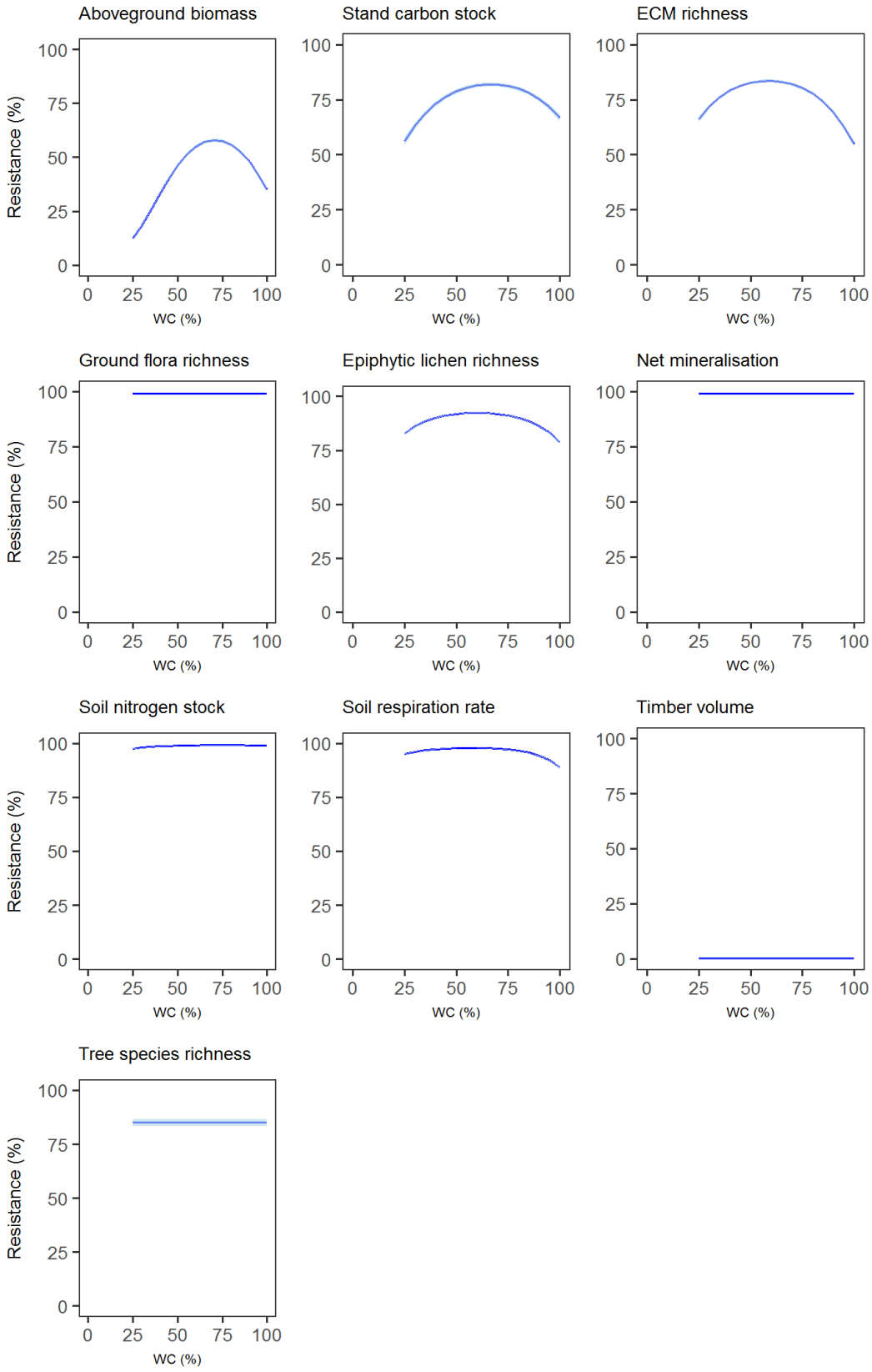


Fig. A5.23. Results of the most parsimonious GLMs for resistance of the different ecosystem properties across the woodland cover (WC) gradient resulting from PDI3 with 0% WC excluded. The blue lines represent the most parsimonious model for all EPs, and the blue surrounds represent the 95% confidence intervals of the most parsimonious model.

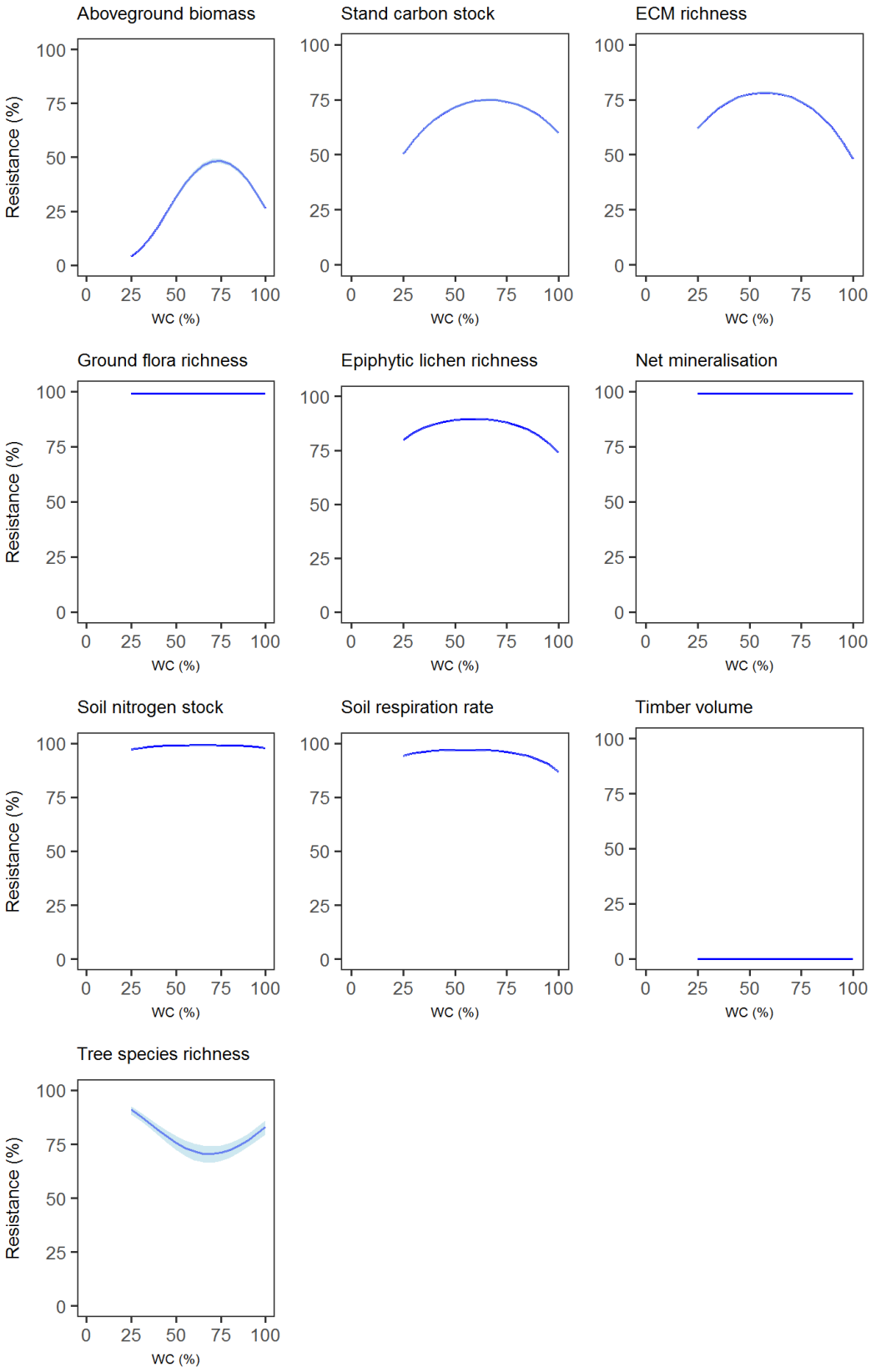


Fig. A5.24. Results of the most parsimonious GLMs for resistance of the different ecosystem properties across the woodland cover (WC) gradient resulting from PDI4 with 0% WC excluded. The blue lines represent the most parsimonious model for all EPs, and the blue surrounds represent the 95% confidence intervals of the most parsimonious model.

Effect of woodland cover on persistence

The initial WC had an effect on the persistence of three EPs under PDI1 scenario, six under PDI2, seven under PDI3 and four EPs in the PDI4. Thus, WC influenced the resistance of 20/40 EPs altogether. When there was no pulse disturbance, WC had a significant effect on zero EPs between 30 and 170 years (Table A5.22; Figs A5.25–5.28).

Table A5.22: The most parsimonious models for persistence and associated measures of parsimony (Log likelihood, AIC), support (ΔAIC, AIC weight) and goodness of fit (r^2_{adj}) with 0% WC excluded. WC and WC^2 indicate that linear and quadratic terms of woodland cover were used in the most parsimonious models, respectively. H indicates that the press disturbance (i.e. herbivory) was included as a term in the most parsimonious model. Null indicates that the null model was the most parsimonious. PDI indicates the intensity of disturbance the ecosystem properties were measured in response to.

Persistence					
Ecosystem property	**Model structure**	**Log likelihood**	**ΔAIC**	**AIC Weight**	r^2_{adj}
PDI1					
AGB	Null	789.398	0	1	0
Carbon	Null	-24.237	0	0.48	0
ECM	Null	789.398	0	1	0
GF	WC*H+WC^2	-23.181	9.101	0.515	0.919
Lichen	Null	789.398	0	1	0
Net min	WC+WC^2+H	-21.78	16.675	0.832	0.898
Nitrogen	Null	-22.458	0	0.504	0
SRR	Null	789.398	0	1	0
Timber	Null	789.398	0	1	0
Tree species	WC	-11.718	9.84	0.852	0.624
PDI2					
AGB	WC+WC^2	-35.398	7.095	0.354	0.787
Carbon	Null	-36.725	0	0.293	0
ECM	WC	-33.784	4.07	0.393	0.476
GF	WC+WC^2+H	-26.276	22.761	0.969	0.917
Lichen	Null	-26.747	0	0.463	0
Net min	WC+WC^2+H	-25.689	16.369	0.943	0.891
Nitrogen	Null	-14.334	0	0.603	0
SRR	Null	-18.855	0	0.549	0
Timber	WC+WC^2	-32.771	23.456	0.812	0.897
Tree species	WC	7.767	30.325	0.97	0.856
PDI3					
AGB	WC+WC^2+H	-35.212	19.074	0.96	0.891
Carbon	WC+WC^2+H	-18.11	46.429	0.998	0.973
ECM	WC+WC^2+H	-25.991	23.469	0.997	0.92

GF	H	-33.103	6.208	0.953	0.318
Lichen	$WC+WC^2+H$	-18.43	24.474	0.993	0.93
Net min	H	-27.7	5.789	0.945	0.32
Nitrogen	$WC+WC^2$	-23.97	16.254	0.797	0.869
SRR	$WC+WC^2+H$	-8.988	28.941	0.999	0.949
Timber	H	-37.276	0.988	0.46	0.137
Tree species	WC	10.93	27.305	0.964	0.838
PDI4					
AGB	H	-46.489	8.112	0.528	0.338
Carbon	Null	-47.73	0	0.604	0
ECM	$WC+WC^2+H$	-35.368	6.746	0.563	0.815
GF	Null	-23.567	0	0.545	0
Lichen	$WC+WC^2+H$	-27.262	7.219	0.623	0.836
Net min	Null	-15.564	0	0.629	0
Nitrogen	$WC+WC^2$	-23.119	26.703	0.919	0.917
SRR	$WC+WC^2+H$	-9.848	24.86	0.854	0.939
Timber	Null	780.795	0	1	0
Tree species	Null	-6.672	0	0.644	0
PDI0					
AGB	Null	789.398	0	1	0
Carbon	Null	789.398	0	1	0
ECM	Null	789.398	0	1	0
GF	H	-12.332	4.855	0.917	0.334
Lichen	Null	789.398	0	1	0
Net min	H	-11.258	6.225	0.953	0.374
Nitrogen	Null	789.398	0	1	0
SRR	Null	789.398	0	1	0
Timber	Null	789.398	0	1	0
Tree species	Null	-27.4	0	0.818	0

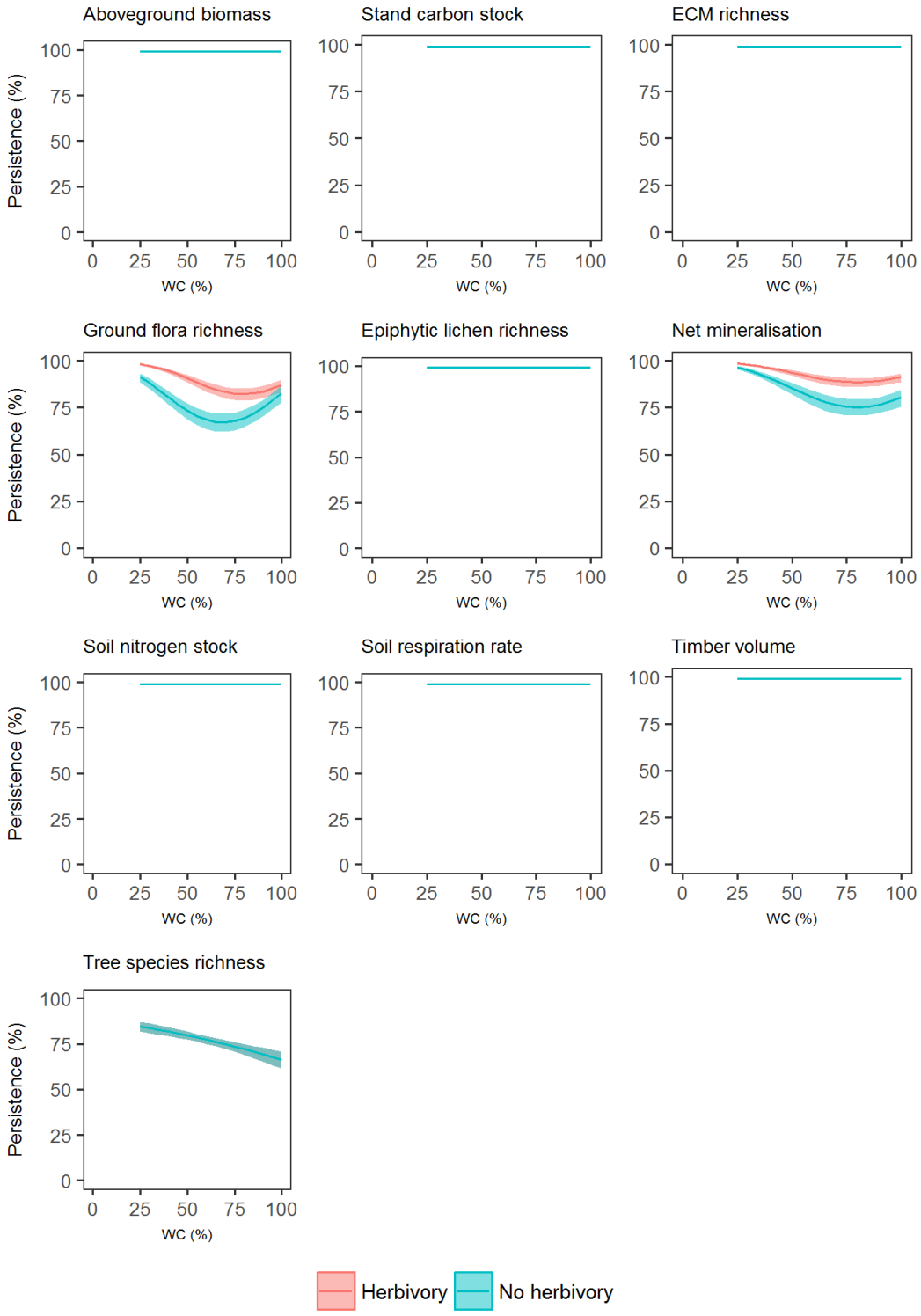


Fig. A5.25. Results of the most parsimonious GLMs for persistence of the different ecosystem properties across the woodland cover (WC) gradient resulting from PDI1 with 0% WC excluded. The red and blue lines and surrounds represent the most parsimonious model, with and without herbivory, respectively. The coloured surrounds represents the 95% confidence intervals of the most parsimonious model. Note: where herbivory did not have a significant effect in the most parsimonious model both lines and confidence intervals overlap, with the only the blue lines and surrounds showing.

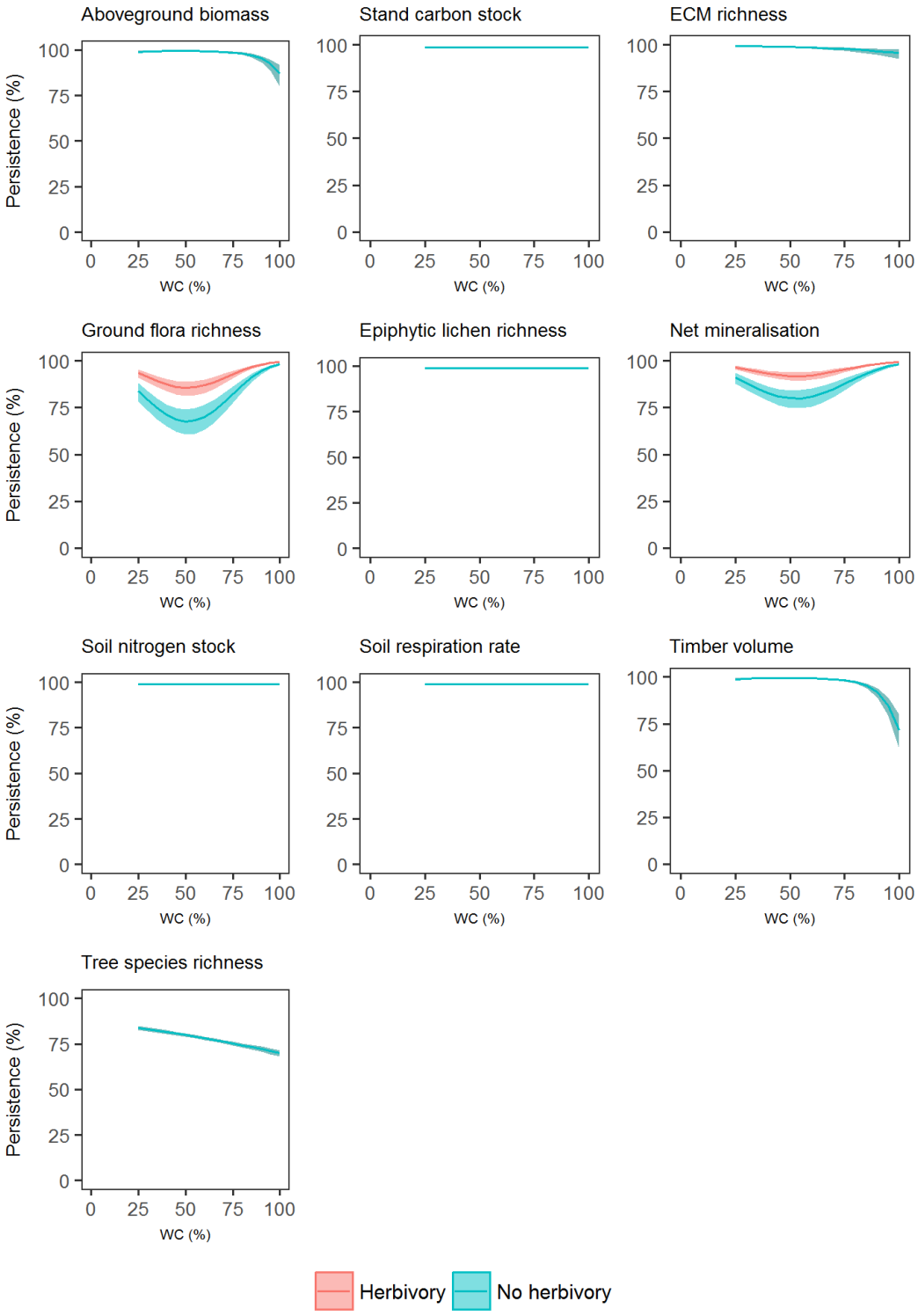


Fig. A5.26. Results of the most parsimonious GLMs for persistence of the different ecosystem properties across the woodland cover (WC) gradient resulting from PDI2 with 0% WC excluded. The red and blue lines and surrounds represent the most parsimonious model, with and without herbivory, respectively. The coloured surrounds represent the 95% confidence intervals of the most parsimonious model. Note: where herbivory did not have a significant effect in the most parsimonious model both lines and confidence intervals overlap, with the only the blue lines and surrounds showing.

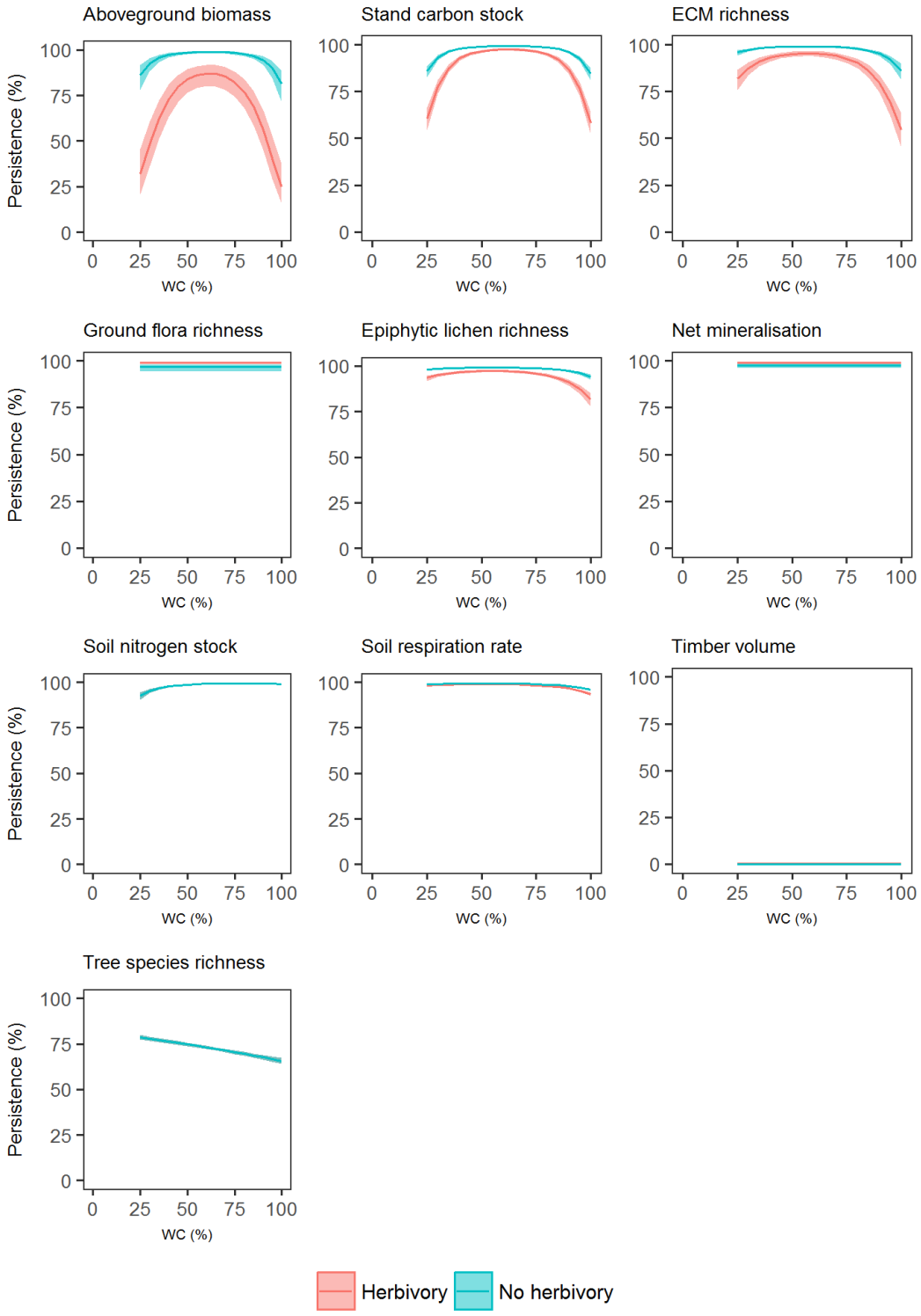


Fig. A5.27. Results of the most parsimonious GLMs for persistence of the different ecosystem properties across the woodland cover (WC) gradient resulting from PDI3 with 0% WC excluded. The red and blue lines and surrounds represent the most parsimonious model, with and without herbivory, respectively. The coloured surrounds represent the 95% confidence intervals of the most parsimonious model. Note: where herbivory did not have a significant effect in the most parsimonious model both lines and confidence intervals overlap, with the only the blue lines and surrounds showing.

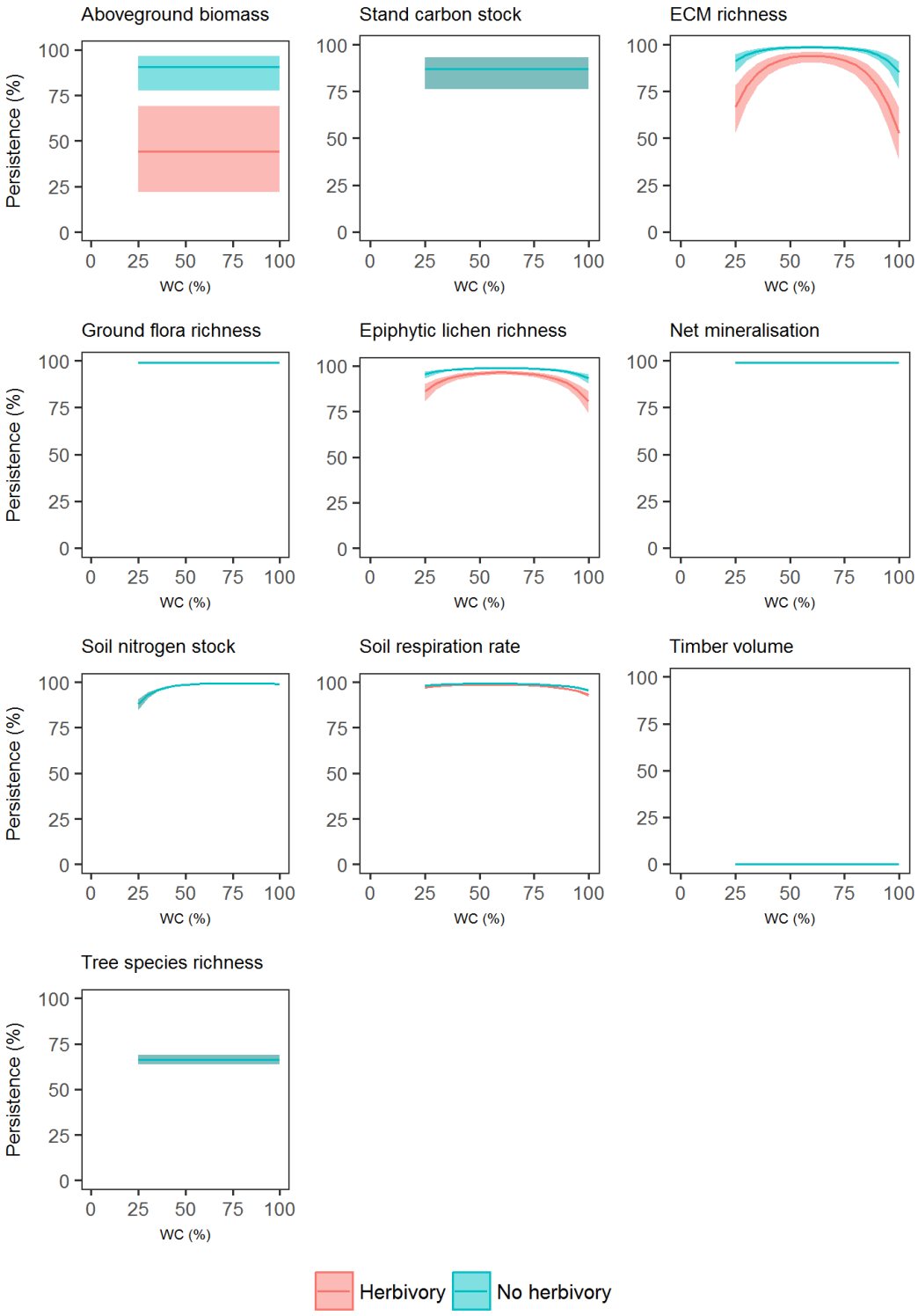


Fig. A5.28. Results of the most parsimonious GLMs for persistence of the different ecosystem properties across the woodland cover (WC) gradient resulting from PDI4 with 0% WC excluded. The red and blue lines and surrounds represent the most parsimonious model, with and without herbivory, respectively. The coloured surrounds represent the 95% confidence intervals of the most parsimonious model. Note: where herbivory did not have a significant effect in the most parsimonious model both lines and confidence intervals overlap, with the only the blue lines and surrounds showing.

Effect of woodland cover on recovery time

The initial WC had an effect on the recovery time of 10 EPs under PDI1, nine EPs under PDI2, and six EPs under PDI3 and PDI4. Thus, WC influenced the recovery of 31/40 EPs altogether. For PDI4, there was a sharp incline for EPs that were influenced by WC between the 0% and 25% WC, after which most reached the maximum recovery time (i.e. 150 years) when herbivory was significant. WC influenced the trajectory of four EPs when there was no pulse disturbance (Table A5.23; Figs A5.29–5.212).

Table A5.23: The most parsimonious models for recovery time fitted and associated measures of parsimony (Log likelihood, AIC), support (ΔAIC, AIC weight) and goodness of fit (r^2_{adj}) with 0% WC excluded. WC and WC^2 indicate that linear and quadratic terms of woodland cover were used in the most parsimonious models, respectively. H indicates that the press disturbance (i.e. herbivory) was included as a term in the most parsimonious model. WC*H indicates that a significant interaction between WC and herbivory was included in the most parsimonious model. Null indicates that the null model was the most parsimonious. PDI indicates the intensity of disturbance that the response of the ecosystem properties was measured in response to.

Recovery					
Ecosystem property	**Model structure**	**Log likelihood**	**ΔAIC**	**AIC Weight**	**r^2_{adj}**
PDI1					
AGB	$WC+WC^2+H$	-47.201	680.975	0.814	0.938
Carbon	$WC+WC^2+H$	-41.874	1745.721	0.679	0.942
ECM	$WC+WC^2+H$	-47.201	680.975	0.814	0.938
GF	$WC*H+WC^2$	-317.984	1721.757	1	0.867
Lichen	$WC+WC^2+H$	-47.201	680.975	0.814	0.938
Net min	$WC*H+WC^2$	-317.984	1721.757	1	0.867
Nitrogen	$WC+WC^2+H$	-41.815	2076.774	0.821	0.95
SRR	$WC+WC^2+H$	-47.201	680.975	0.814	0.938
Timber	$WC+WC^2$	-106.74	630.966	0.795	0.726
Tree species	$WC*H+WC^2$	-264.572	157.898	1	0.503
PDI2					
AGB	$WC*H+WC^2$	-84.702	1506.675	0.581	0.973
Carbon	$WC*H+WC^2$	-91.283	1550.603	0.992	0.982
ECM	$WC*H+WC^2$	-84.702	1506.675	0.581	0.973
GF	$WC*H+WC^2$	-87.567	2401.321	1	0.812
Lichen	$WC*H+WC^2$	-94.188	1643.882	0.503	0.831
Net min	$WC*H+WC^2$	-99.81	1555.981	1	0.381
Nitrogen	$WC*H+WC^2$	-41.737	2003.35	0.835	0.949
SRR	$WC*H+WC^2$	-84.702	1506.675	0.581	0.973

Timber	WC*H+WC^2	-91.848	643.394	0.411	0.919
Tree species	Null	921.515	0	1	0
PDI3					
AGB	WC+WC^2+H	-243.784	467.243	0.606	0.705
Carbon	WC+WC^2+H	-134.533	1047.836	0.737	0.866
ECM	WC+WC^2+H	-242.853	461.6	0.632	0.704
GF	Null	921.515	0	1	0
Lichen	WC+WC^2+H	-266.839	522.973	0.667	0.717
Net min	Null	921.515	0	1	0
Nitrogen	WC+WC^2	-42.179	2315.701	0.812	0.953
SRR	WC+WC^2+H	-242.853	461.6	0.632	0.704
Timber	Null	921.515	0	1	0
Tree species	Null	921.515	0	1	0
PDI4					
AGB	WC+WC^2+H	-163.844	207.028	0.854	0.655
Carbon	WC+WC^2+H	-232.095	228.749	0.836	0.479
ECM	WC+WC^2+H	-163.844	207.028	0.854	0.655
GF	Null	921.515	0	1	0
Lichen	WC+WC^2+H	-163.844	207.028	0.854	0.655
Net min	Null	921.515	0	1	0
Nitrogen	WC+WC^2	-42.179	2315.701	0.812	0.953
SRR	WC+WC^2+H	-163.844	207.028	0.854	0.655
Timber	Null	921.515	0	1	0
Tree species	Null	921.515	0	1	0
PDI0					
AGB	Null	921.515	0	1	0
Carbon	Null	921.515	0	1	0
ECM	Null	921.515	0	1	0
GF	Null	921.515	0	1	0
Lichen	Null	921.515	0	1	0
Net min	Null	921.515	0	1	0
Nitrogen	Null	921.515	0	1	0
SRR	Null	921.515	0	1	0
Timber	Null	921.515	0	1	0
Tree species	WC*H+WC^2	-941.908	577.641	0.999	0.315

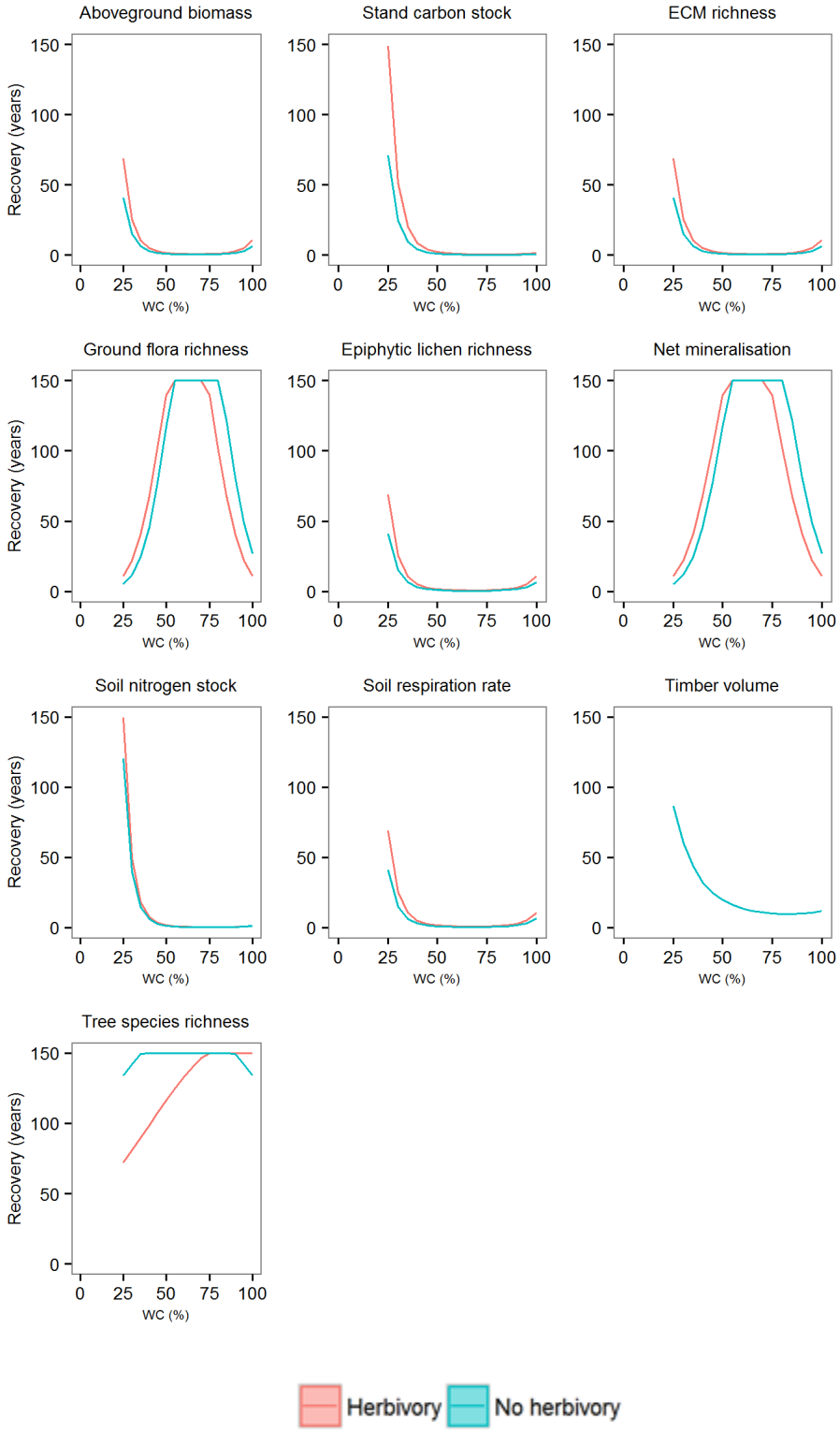


Fig. A5.29. Results of the most parsimonious GLMs for recovery time of the different ecosystem properties across the woodland cover (WC) gradient resulting from PDI1 with 0% WC excluded. The red and blue lines and surrounds represent the most parsimonious model, with and without herbivory, respectively. The coloured surrounds represent the 95% confidence intervals of the most parsimonious model. Note: where herbivory did not have a significant effect in the most parsimonious model both lines and confidence intervals overlap, with the only the blue lines and surrounds showing.

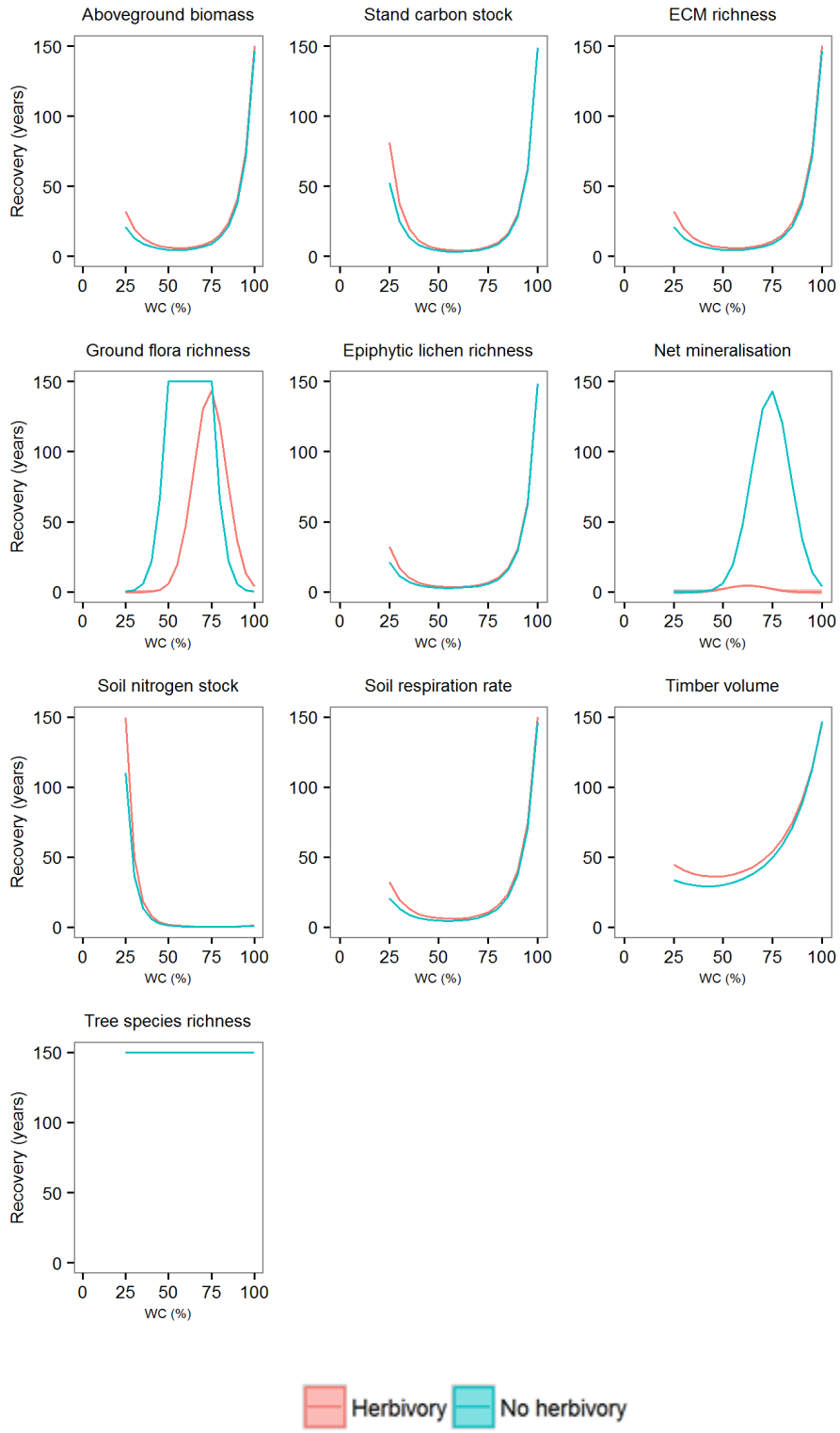


Fig. A5.210. Results of the most parsimonious GLMs for recovery time of the different ecosystem properties across the woodland cover (WC) gradient resulting from PDI2 with 0% WC excluded. The red and blue lines and surrounds represent the most parsimonious model, with and without herbivory, respectively. The coloured surrounds represent the 95% confidence intervals of the most parsimonious model. Note: where herbivory did not have a significant effect in the most parsimonious model both lines and confidence intervals overlap, with the only the blue lines and surrounds showing.

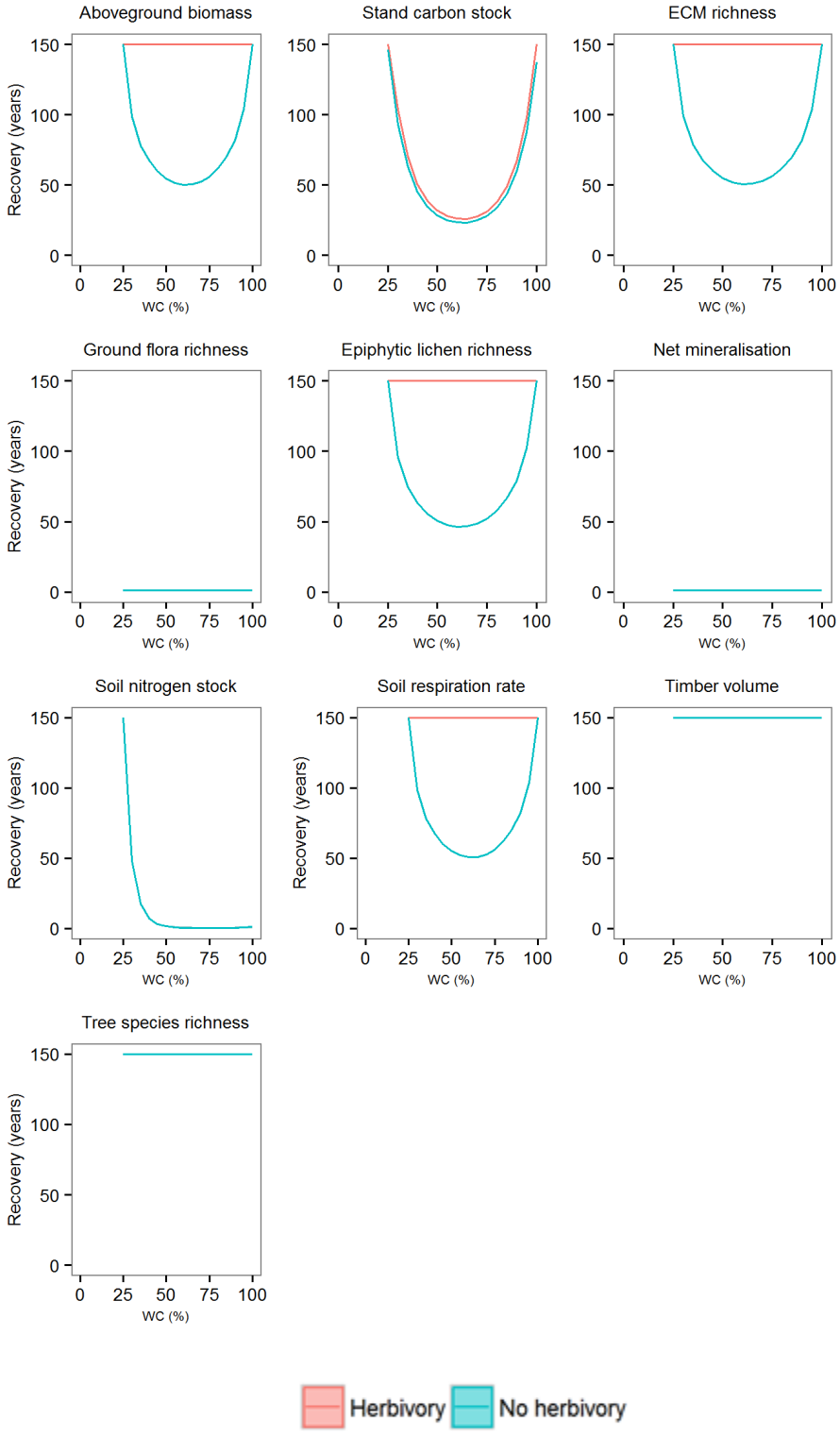


Fig. A5.211. Results of the most parsimonious GLMs for recovery time of the different ecosystem properties across the woodland cover (WC) gradient resulting from PDI3 with 0% WC excluded. The red and blue lines and surrounds represent the most parsimonious model, with and without herbivory, respectively. The coloured surrounds represent the 95% confidence intervals of the most parsimonious model. Note: where herbivory did not have a significant effect in the most parsimonious model both lines and confidence intervals overlap, with the only the blue lines and surrounds showing.

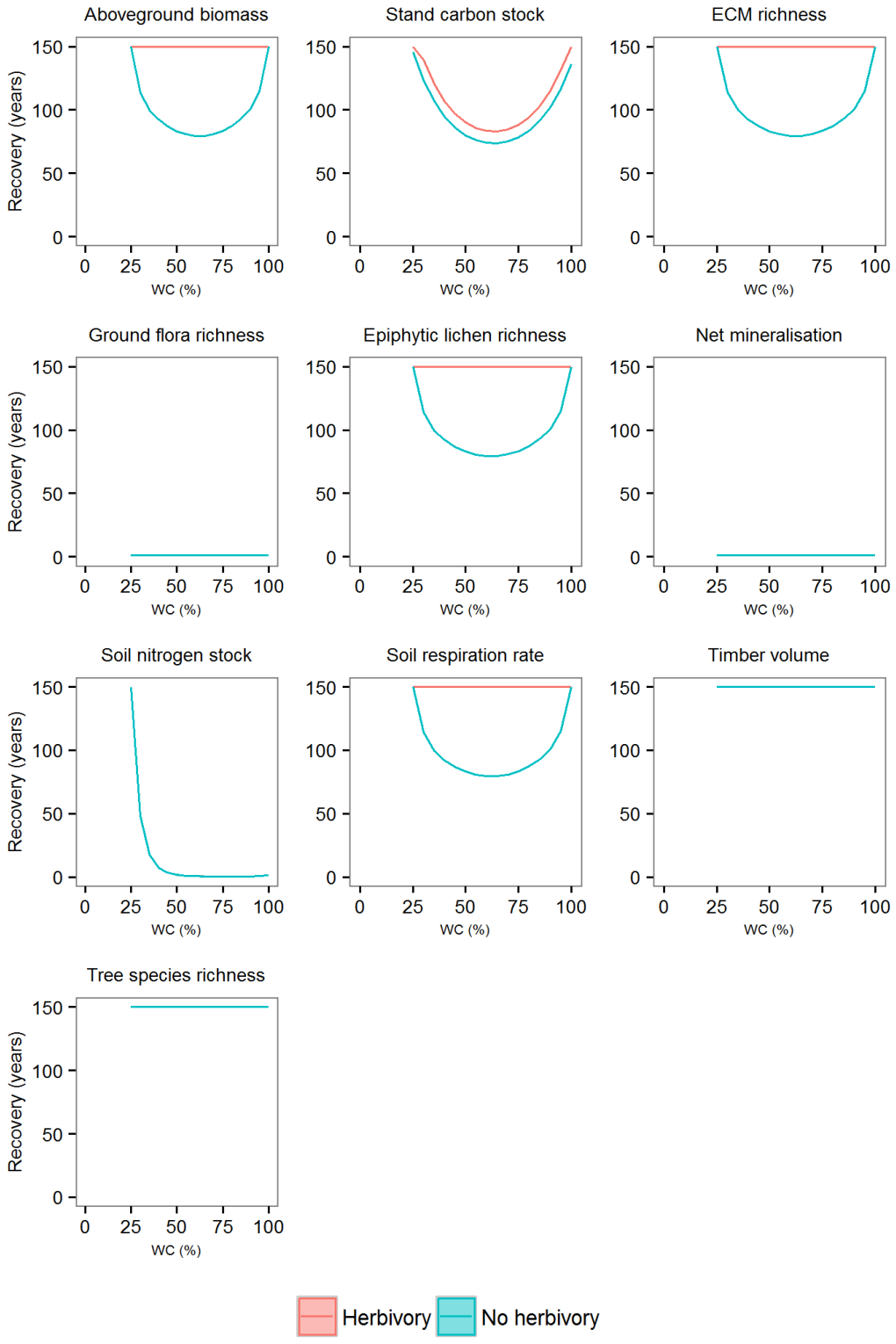


Fig. A5.212. Results of the most parsimonious GLMs for recovery time of the different ecosystem properties across the woodland cover (WC) gradient resulting from PDI4 with 0% WC excluded. The red and blue lines and surrounds represent the most parsimonious model, with and without herbivory, respectively. The coloured surrounds represent the 95% confidence intervals of the most parsimonious model. Note: where herbivory did not have a significant effect in the most parsimonious model both lines and confidence intervals overlap, with the only the blue lines and surrounds showing.

Appendix 5.3: Summary of the effect of WC on resilience with 0% WC excluded

Table A5.3: Summary table of the influence of woodland cover (WC) on the individual resilience attributes with 0% WC excluded. PDI indicates the pulse disturbance intensity that the resistant attribute was measured in response to. The number in each column relates to how many EPs included those terms in the most parsimonious models. The 'No WC relationship' column indicates the numbers of times the most parsimonious model did not include a WC term, or where the $\Delta AIC < 4$ compared to the null model, in accordance with the *a priori* criteria. The Total rows are the sum of the of the four PDI that included a pulse disturbance (i.e. not PDI0), and these numbers are out of 40, which relates to the EPs multiplied by the number of PDI scenarios that involved a pulse disturbance. H and WC*H indicate whether there was a significant effect of herbivory or a significant interaction between H and WC, respectively.

Resilience attribute	PDI scenario	No WC relationship	WC (linear)	WC (Non-linear)	Total WC models for each PDI	H	WC*H
Resistance	PDI1	4	1	5	6	NA	NA
	PDI2	4	1	5	6	NA	NA
	PDI3	4	0	6	6	NA	NA
	PDI4	4	0	6	6	NA	NA
	Total	**16**	**2**	**22**	**24**	**NA**	**NA**
	PDI0	8	0	2	2	NA	NA
Persistence	PDI1	7	1	2	3	1	7
	PDI2	4	2	4	6	0	4
	PDI3	3	1	6	7	0	3
	PDI4	6	0	4	4	0	6
	Total	**20**	**4**	**16**	**20**	**1**	**20**
	PDI0	10	0	0	0	0	10
Recovery	PDI1	0	0	10	10	3	0
	PDI2	1	0	9	9	9	1
	PDI3	4	0	6	6	0	4
	PDI4	4	0	6	6	0	4
	Total	**9**	**0**	**31**	**31**	**12**	**9**
	PDI0	9	0	1	1	1	9

Appendix 5.4: Bar charts of relationships between woodland cover and the resilience attributes

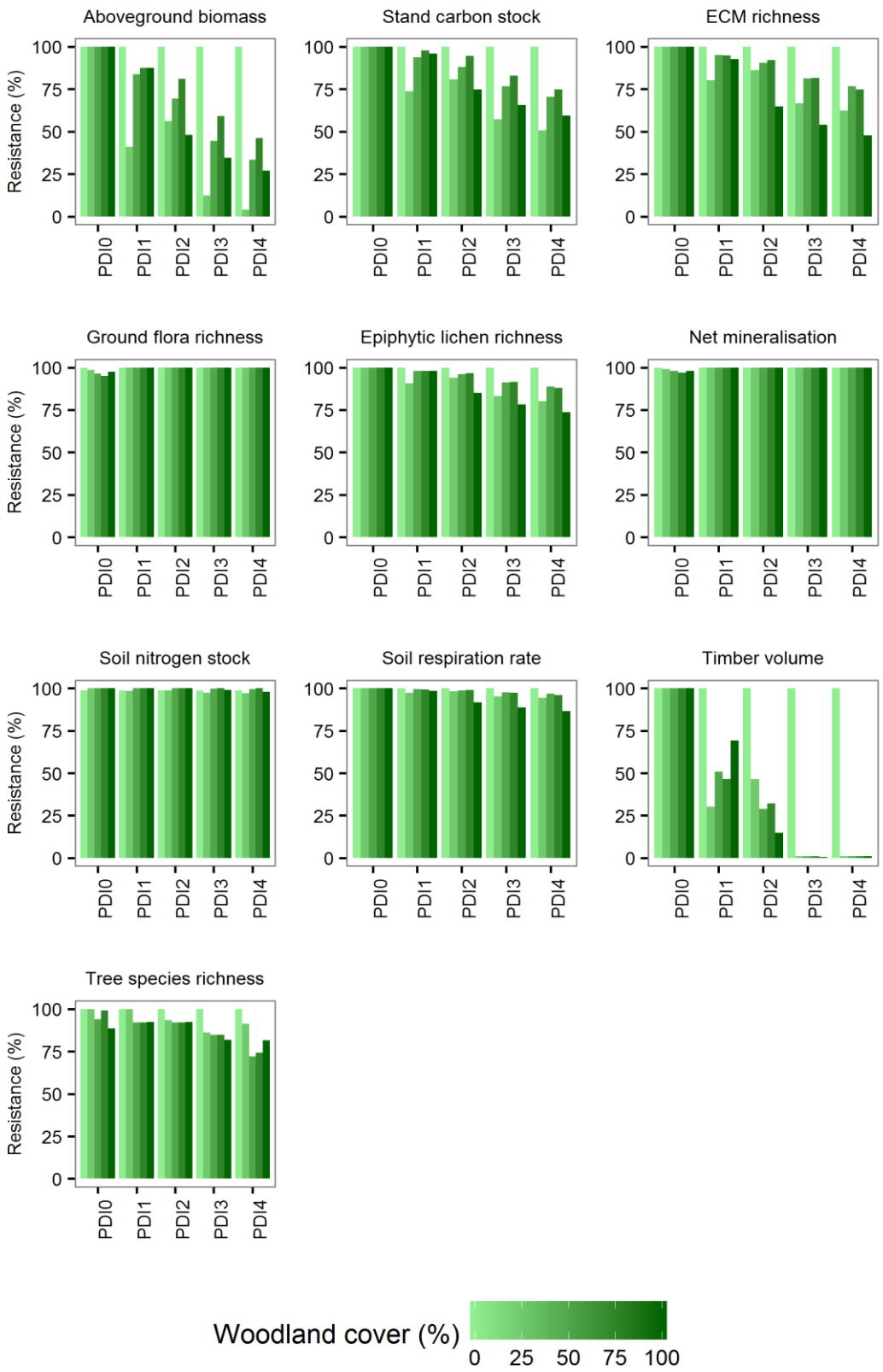


Fig. A5.41: Mean values (n = 6) of resistance for the different ecosystems properties under differing scenarios of pulse disturbance intensity (PDI). The green gradient represents the initial woodland cover percentage of the landscape.

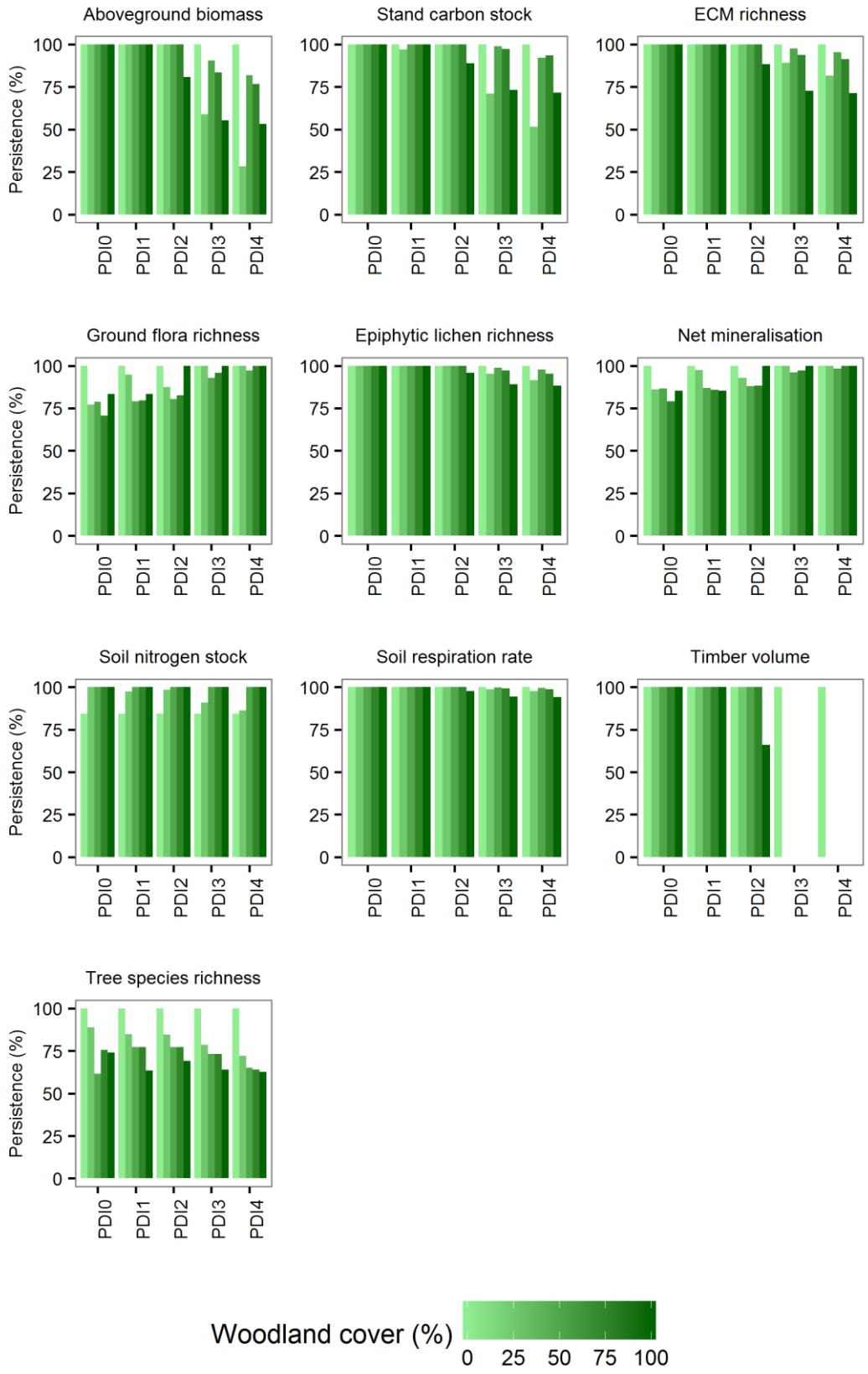


Fig. A5.42: Mean values (n = 6) of persistence for the different ecosystems properties under differing scenarios of pulse disturbance intensity (PDI). The green gradient represents the initial woodland cover percentage of the landscape.

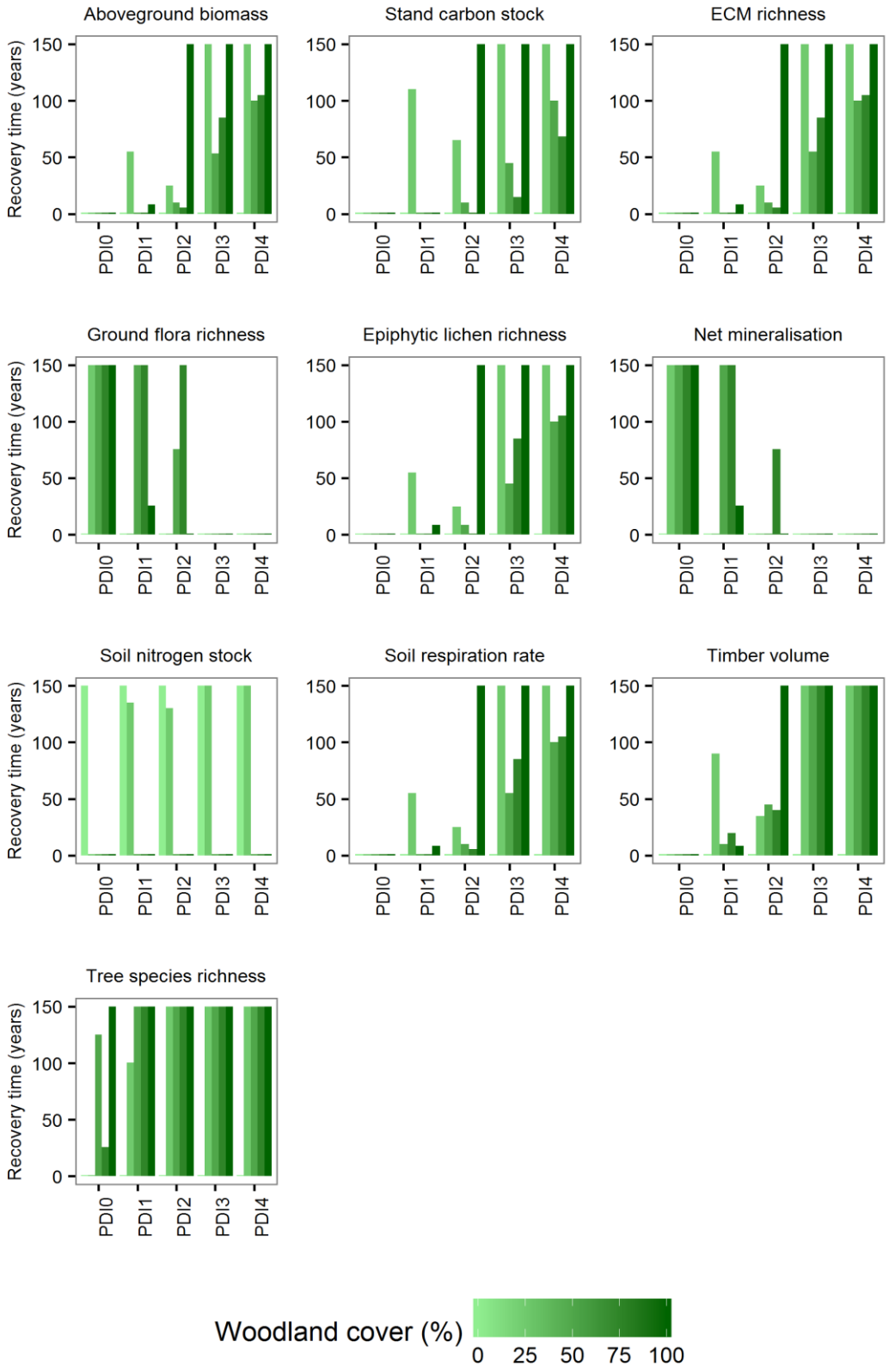


Fig. A5.43: Mean values (n = 6) of recovery time for the different ecosystems properties under differing scenarios of pulse disturbance intensity (PDI). The green gradient represents the initial woodland cover percentage of the landscape.

Appendix 5.5: Species contributions to the initial biomass of the initial woodland cover landscapes.

Table A5.5: Contribution of different species to the biomass of the different percentages of initial woodland cover across a landscape.

Woodland cover (%)	Species	Initial biomass of the landscape (%)
25	Beech	32.140
25	Oak	46.141
25	Other	21.719
50	Beech	26.610
50	Oak	18.341
50	Other	55.049
75	Beech	17.002
75	Oak	13.487
75	Other	69.511
100	Beech	46.633
100	Oak	15.032
100	Other	38.335

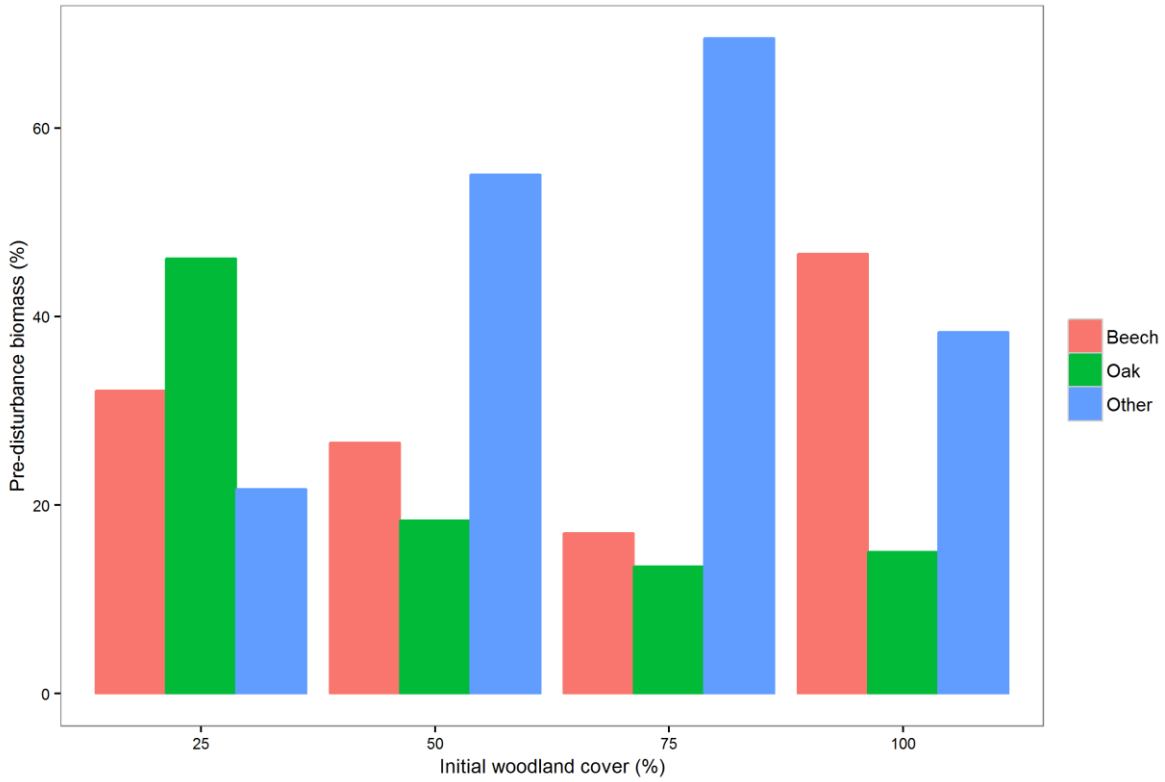


Fig. A5.5: Contribution of different species to the pre-disturbance biomass of the initial woodland cover landscapes. Red represents the percentage of beech, green represents the percentage of oak and blue represents all other species.

Appendix 5.6: Spearman Rank correlations with 0% WC excluded

Table A5.6: Results of Spearman Rank correlations between the different resilience attributes (RAs), persistence (per), resistance (res) and recovery (rec), for all the ecosystem properties tested in this study under the different pulse disturbance intensity (PDI) scenarios with 0% WC excluded. Values shown in bold are considered are significant to the alpha level of 0.005. *r* represents the Spearman's correlation coefficients and r^2 represents the variation explained. A '-' represents correlations that could not be calculated due at least one attribute of resilience not changing across the woodland cover gradient.

Ecosystem property	RAs tested	PDI1			PDI2			PDI3			PDI4			PDI0		
		r	*p*	r^2	*r*	*p*	r^2	*r*	*p*	r^2	*r*	*p*	r^2	*r*	*p*	r^2
AGB	per-rec	-	-	-	-0.769	< 0.001	**0.591**	-0.779	< 0.001	**0.607**	-0.759	< 0.001	**0.576**	-	-	-
	per-res	-	-	-	0.749	< 0.001	**0.561**	0.381	0.067	0.145	0.614	0.001	**0.377**	-	-	-
	res-rec	-0.391	0.059	0.153	-0.890	< 0.001	**0.792**	-0.514	0.010	0.264	-0.377	0.070	0.142	-	-	-
ECM	per-rec	-	-	-	-0.769	< 0.001	**0.591**	-0.778	< 0.001	**0.605**	-0.751	< 0.001	**0.564**	-	-	-
	per-res	-	-	-	0.749	< 0.001	**0.561**	0.594	0.002	**0.353**	0.773	< 0.001	**0.598**	-	-	-
	res-rec	-0.907	< 0.001	**0.823**	-0.890	< 0.001	**0.792**	-0.515	0.010	0.265	-0.439	0.032	0.193	-	-	-
Lichen	per-rec	-	-	-	-0.761	< 0.001	**0.579**	-0.784	< 0.001	**0.615**	-0.759	< 0.001	**0.576**	-	-	-
	per-res	-	-	-	0.753	< 0.001	**0.567**	0.568	0.004	**0.323**	0.662	< 0.001	**0.438**	-	-	-
	res-rec	-0.881	< 0.001	**0.776**	-0.934	< 0.001	**0.872**	-0.492	0.015	0.242	-0.439	0.032	0.193	-	-	-
GF	per-rec	-0.719	< 0.001	**0.517**	-0.620	0.001	**0.384**	-	-	-	-	-	-	-	-	-
	per-res	-	-	-	-	-	-	-	-	-	-	-	-	0.576	0.003	**0.332**
	res-rec	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Net min	per-rec	-0.501	0.013	0.251	-0.578	0.003	0.334	-	-	-	-	-	-	-	-	-
	per-res	-	-	-	-	-	-	-	-	-	-	-	-	0.522	0.009	0.272
	res-rec	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nitrogen	per-rec	-0.754	< 0.001	**0.569**	-0.754	< 0.001	**0.569**	-0.987	< 0.001	**0.974**	-0.987	< 0.001	**0.974**	-	-	-
	per-res	0.750	< 0.001	**0.562**	0.750	< 0.001	**0.562**	0.764	< 0.001	**0.584**	0.757	< 0.001	**0.573**	-	-	-
	res-rec	-0.997	< 0.001	**0.994**	-0.997	< 0.001	**0.994**	-0.757	< 0.001	**0.573**	-0.751	< 0.001	**0.564**	-	-	-
SRR	per-rec	-	-	-	-0.769	< 0.001	**0.591**	-0.778	< 0.001	**0.605**	-0.751	< 0.001	**0.564**	-	-	-
	per-res	-	-	-	0.749	< 0.001	**0.561**	0.641	0.001	**0.411**	0.804	< 0.001	**0.646**	-	-	-
	res-rec	-0.907	< 0.001	**0.823**	-0.890	< 0.001	**0.792**	-0.623	0.001	**0.388**	-0.439	0.032	0.193	-	-	-
Carbon	per-rec	-0.754	< 0.001	**0.569**	-0.760	< 0.001	**0.578**	-0.838	< 0.001	**0.702**	-0.828	< 0.001	**0.686**	-	-	-
	per-res	0.574	0.003	**0.329**	0.739	< 0.001	**0.546**	0.736	< 0.001	**0.542**	0.790	< 0.001	**0.624**	-	-	-
	res-rec	-0.759	< 0.001	**0.576**	-0.951	< 0.001	**0.904**	-0.883	< 0.001	**0.780**	-0.565	0.004	**0.319**	-	-	-
Timber	per-rec	-	-	-	-0.800	< 0.001	**0.640**	-	-	-	-	-	-	-	-	-
	per-res	-	-	-	0.749	< 0.001	**0.561**	0.615	0.001	**0.378**	-	-	-	-	-	-
	res-rec	-0.910	< 0.001	**0.828**	-0.799	< 0.001	**0.638**	-	-	-	-	-	-	-	-	-
Tree species	per-rec	-0.480	0.018	0.230	-	-	-	-	-	-	-	-	-	-0.867	< 0.001	**0.752**
	per-res	0.575	0.003	**0.331**	0.314	0.135	0.099	0.367	0.078	0.135	0.407	0.048	0.166	0.701	< 0.001	**0.491**
	res-rec	-0.357	0.087	0.127	-	-	-	-	-	-	-	-	-	-0.927	< 0.001	**0.859**

Appendix 5.7: Changes in the mean aboveground biomass for the different initial woodland cover landscapes resulting from the different pulse disturbances intensity scenarios

Table A5.7: Changes in the mean aboveground biomass (AGB) for the different initial woodland cover landscapes resulting from the different pulse disturbances intensity (PDI) scenarios. Pre-disturbance represents the mean AGB at year 15 (i.e. the last timestep before the disturbance); post-disturbance represents the mean AGB at year 20 (i.e. the first timestep after the pulse disturbance); 'Difference in AGB' and 'AGB change' represent the difference between pre and post disturbance AGB values and the corresponding percentage change, respectively. All AGB values are mean values. The standard deviation of each value is shown in brackets.

		Aboveground biomass (Mg ha^{-1})			
PDI scenario	**Woodland cover (%)**	**Pre-disturbance**	**Post-disturbance**	**Difference in AGB**	**AGB change (%)**
PDI0	0	0 (+/- 0)	0 (+/- 0)	0 (+/- 0)	0 (+/- 0)
PDI1	0	0 (+/- 0)	0 (+/- 0)	0 (+/- 0)	0 (+/- 0)
PDI2	0	0 (+/- 0)	0 (+/- 0)	0 (+/- 0)	0 (+/- 0)
PDI3	0	0 (+/- 0)	0 (+/- 0)	0 (+/- 0)	0 (+/- 0)
PDI4	0	0 (+/- 0)	0 (+/- 0)	0 (+/- 0)	0 (+/- 0)
PDI0	25	69.521 (+/- 0.026)	72.501 (+/- 0.043)	2.981 (+/- 0.026)	4.286 (+/- 0.024)
PDI1	25	69.511 (+/- 0.003)	40.493 (+/- 0.002)	-29.018 (+/- 0.003)	-41.746 (+/- 0.002)
PDI2	25	69.531 (+/- 0.004)	50.07 (+/- 0.007)	-19.462 (+/- 0.004)	-27.99 (+/- 0.005)
PDI3	25	69.532 (+/- 0.002)	15.369 (+/- 0.004)	-54.163 (+/- 0.002)	-77.897 (+/- 0.005)
PDI4	25	69.512 (+/- 0.002)	5.321 (+/- 0.002)	-64.191 (+/- 0.002)	-92.345 (+/- 0.002)
PDI0	50	71.996 (+/- 10.082)	79.255 (+/- 9.702)	7.259 (+/- 10.082)	9.125 (+/- 1.614)
PDI1	50	71.033	64.706	-6.327	-8.908

		(+/- 0.009)	(+/- 0.011)	(+/- 0.009)	(+/- 0.006)
PDI2	50	71.039 (+/- 0.006)	58.191 (+/- 0.012)	-12.848 (+/- 0.006)	-18.086 (+/- 0.010)
PDI3	50	71.042 (+/- 0.005)	43.779 (+/- 0.008)	-27.263 (+/- 0.005)	-38.376 (+/- 0.008)
PDI4	50	71.043 (+/- 0.004)	35.566 (+/- 0.003)	-35.477 (+/- 0.004)	-49.937 (+/- 0.004)
PDI0	75	119.151 (+/- 7.017)	129.118 (+/- 7.083)	9.967 (+/- 7.017)	8.175 (+/- 0.403)
PDI1	75	118.102 (+/- 0.01)	110.256 (+/- 0.011)	-7.847 (+/- 0.01)	-6.644 (+/- 0.002)
PDI2	75	118.098 (+/- 0.005)	105.773 (+/- 0.013)	-12.326 (+/- 0.005)	-10.437 (+/- 0.007)
PDI3	75	118.1 (+/- 0.003)	87.713 (+/- 0.008)	-30.387 (+/- 0.003)	-25.73 (+/- 0.005)
PDI4	75	118.117 (+/- 0.026)	74.622 (+/- 0.275)	-43.495 (+/- 0.026)	-36.823 (+/- 0.219)
PDI0	100	286.23 (+/- 0.002)	290.502 (+/- 0.003)	4.272 (+/- 0.002)	1.492 (+/- 0.001)
PDI1	100	286.229 (+/- 0.002)	267.388 (+/- 0.056)	-18.841 (+/- 0.002)	-6.583 (+/- 0.019)
PDI2	100	286.23 (+/- 0.001)	185.596 (+/- 0.066)	-100.633 (+/- 0.001)	-35.158 (+/- 0.023)
PDI3	100	286.229 (+/- 0.001)	146.873 (+/- 0.069)	-139.356 (+/- 0.001)	-48.687 (+/- 0.024)
PDI4	100	286.232 (+/- 0.002)	121.148 (+/- 0.035)	-165.084 (+/- 0.002)	-57.675 (+/- 0.013)

References for Appendices

AntWeb, 2015. *AntWeb* [online]. Available from: https://www.antweb.org [Accessed March 2015].

Bazely, D. R., Myers, J. H. and da Silva, K. B., 1991. The response of numbers of bramble prickles to herbivory and depressed resource availability. *Oikos,* 61, 327-336.

Bergström, R. and Guillet, C., 2002. Summer browsing by large herbivores in short-rotation willow plantations. *Biomass Bioenergy,* 23, 27-32.

British Arachnological Society. *Spider and harvestman recording scheme* [online]. Available from: http://srs.britishspiders.org.uk [Accessed March 2015].

Campbell, D., Swanson, G. M. and Sales, J., 2004. Methodological insights: comparing the precision and cost-effectiveness of faecal pellet group count methods. *Journal of Applied Ecology,* 41, 1185-1196.

Cantarello, E. and Newton, A. C., 2008. Identifying cost-effective indicators to assess the conservation status of forested habitats in Natura 2000 sites. *Forest Ecology and Management,* 256 (4), 815-826.

de Jong, Y., Verbeek, M., Michelsen, V., de Place Bjørn, P., Los, W., Steeman, F., Bailly, N., Basire, C., Chylarecki, P., Stloukal, E. and Hagedorn, G., 2014. Fauna Europaea–all European animal species on the web. *Biodiversity Data Journal*, 2, e4034.

Deluca, T., Zewdie, S., Zackrisson, O., Healey, J. and Jones, D., 2013. Bracken fern (*Pteridium aquilinum* L. kuhn) promotes an open nitrogen cycle in heathland soils. *Plant and Soil,* 367 (1-2), 521-534.

Gibson, D. J., 2002. *Methods in comparative plant population ecology*. Oxford, UK: Oxford University Press.

Husch, B., Beers, T. W. and Kershaw, J. A., 2003. *Forest mensuration* New York, USA: Wiley.

Jenkins, K. J. and Manly, B., 2008. A double-observer method for reducing bias in faecal pellet surveys of forest ungulates. *Journal of Applied Ecology,* 45, 1339-1348.

Jenkins, T. A. R., Mackie, E. D., Matthews, R. W., Miller, G., Randle, T. J. and White, M. E., 2011. *FC woodland carbon code: carbon assessment protocol.* Edinburgh, UK: Forestry Commission.

Keeney, D. R., 1982. Nitrogen-availability indices. *In:* Black, C. A., Evans, D.D., White, J.L., Ensminger, L.E. and Clark, F.E., eds. *Methods of soil analysis: chemical and microbiological properties*. Madison, Wisconsin, USA: Soil Society of America.

Marques, F. F., Buckland, S. T., Goffin, D., Dixon, C. E., Borchers, D. L., Mayle, B. A. and Peace, A. J., 2001. Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland. *Journal of Applied Ecology,* 38 (2),349-363.

Matthews, G. A. R., 1993. *The carbon content of trees*. Edinburgh, UK: Forestry Commission. Forestry Commission technical paper 4.

McKay, H., Hudson, J. B. and Hudson, R. J., 2003. *Woodfuel resource in Britain: appendices*. Edinburgh, UK: Forestry Contracting Association.

Miranda, K. M., Espey, M. G. and Wink, D. A., 2001. A rapid, simple spectrophotometric method for simultaneous detection of nitrate and nitrite. *Nitric Oxide*, 5, 62-71.

NBN Gateway, 2015. *National Biodiversity Networks Gateway* [online]. Available from: https://data.nbn.org.uk/ [Accessed March 2015].

Nentwig W, Blick T, Gloor D, Hänggi A, Kropf C. *Spiders of Europe* [online]. Available from: www.araneae.unibe.ch [Accessed March 2015].
PP Systems, 2010. *EGM-4 Environmental Gas Monitor for CO_2: Operator's manual version 4.18*. New York, USA: PP Systems.
Rowell, D. L., 1994. *Soil science: methods and applications.* Harlow, UK: John Wiley and Sons, Ltd.
Stewart, K. E. J., Bourn, N. A. D. and Thomas, J., 2001. A. An evaluation of three quick methods commonly used to assess sward height in ecology. *Journal of Applied Ecology***,** 38, 1148-1154
Strickler, G. S., 1959. *Use of the densiometer to estimate density of forest canopy on permanent sample plots*. Portland, Oregon, USA: USDA Forest Service.
van Laar, A. and Akça, A., 2007. *Forest mensuration*. Göttingen, Germany: Springer.
Ver Hoef, J. M. and Boveng, P. L., 2007. Quasi-Poisson vs. negative binomial regression: how should we model overdispersed count data? *Ecology*, 88 (11), 2766-2772.